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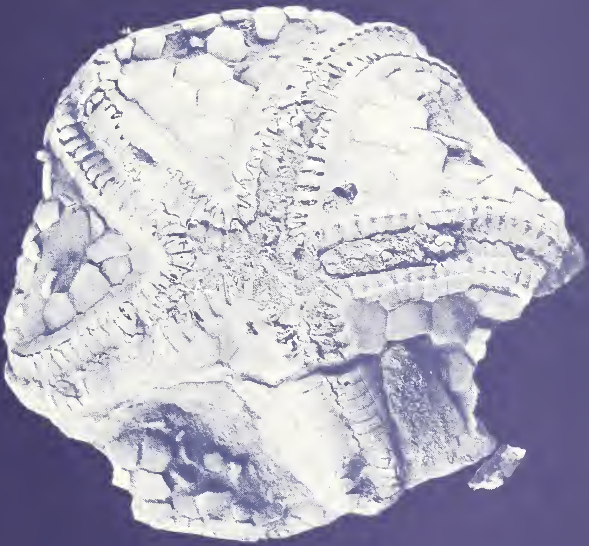

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Cover: *Edriophus levis* (Bather, 1914) from the Middle Ordovician Trenton Group of Kirkfield, Ontario. × 2·5. Specimen in the Smithsonian Institution; photograph by H. B. Whittington.

SUCCESSION AND DIVERSITY IN THE PLEISTOCENE CORAL REEFS OF THE KENYA COAST

by J. A. CRAME

ABSTRACT. Many of the faunal changes that occur in vertical sections through the late Pleistocene coral reefs of the Kenya coast can be interpreted within the context of ecological succession. A number of instances of one set of species 'preparing the ground' for the next were found but these are all restricted to the earliest stages of primary successions. Clearly defined vertical zones are rare and much of the succession on established reefs appears to have been rather random and unstructured. However, this is precisely what some modern theories predict.

Some pattern is provided to early succession by a series of competitive replacements that typically result in domination by faster-growing branching and platy-encrusting species, especially acroporids. Longer-term trends are more cryptic, but there is some evidence to suggest that branching assemblages may eventually be replaced by assemblages of large doming-massive corals.

Diversity is largely controlled by localized environmental disturbances which promote the establishment of either mixed or monospecific coral stands. In a few instances diversity increases continually through succession, and it would appear that 'equilibrium' coral assemblages can be built up within a comparatively short period of reef growth.

THERE is much scope for palaeontologists to interpret some of the many vertical sequences at their disposal in terms of ecological succession (e.g. Valentine 1973, p. 324; Gould 1976, p. 225). Previous emphasis in vertical faunal studies has traditionally been from an evolutionary standpoint, but now many sequences are recognized to be more or less complete records of *in situ* ecological successions. Detailed study of fossil successions, in both reef and non-reef environments (e.g. Johnson 1972; Bretsky and Bretsky 1975, 1976; Walker and Alberstadt 1975; Walker and Parker 1976; Alberstadt and Walker 1976), is leading to the accumulation of valuable data on the mechanisms and rates of community change, much of which can be directly used to test some of the many hypotheses and models of theoretical ecology.

This work concentrates on the study of ecological succession in reef environments and in particular describes the faunal changes revealed in a series of vertical sections through the late Pleistocene coral reefs of the Kenya coast. As a prelude, a brief review is given of previous studies of reef succession and an attempt is made to establish the theoretical framework on which these have been based. Such has been the growth in both theoretical ecology and palaeoecology in recent years that many established theories have been critically reappraised and plausible alternatives suggested. Nowhere is this more so than in the field of community dynamics.

FOSSIL REEF SUCCESSION

Previous studies of fossil reef succession have been profoundly influenced by the seminal work of Lowenstam (1950, 1957) on the Silurian reefs of the Great Lakes area. Based on the physical factors of water depth and wave resistance, Lowenstam delineated three stages in the sequential development of reefs. A reef was established during a quiet-water stage, given substance during the semi-rough-water stage, and finally consolidated into a complex community of interdependent organisms during the rough-water or wave-resistant stage. Nicol (1962) later interpreted these stages

[Palaeontology, Vol. 23, Part 1, 1980, pp. 1-37.]

as the pioneer, pre-climax, and climax stages of an ecological sere. This model of reef development proved intrinsically satisfying to geologists, for many reefs showed a demonstrable increase in complexity through time. New groups of both reef-builders and dwellers were continually incorporated into the framework, and these in turn provided a continual supply of novel biospace for further species to exploit. Frost and Langenheim (1974) recognized pioneer, pre-climax, and climax stages in their analysis of the development of the Oligocene Pueblo Nuevo reef of Mexico, and Mesolella *et al.* (1970) distinguished pioneer deep-water assemblages (with predominantly doming-massive corals) from later shallower-water stages (with predominantly branching corals) in the Pleistocene reefs of Barbados.

Some insight into the methodology that has governed much of the geological research into reef succession can be gained from a recent review by Walker and Alberstadt (1975). These authors analysed the development of eight ancient reef masses in detail (see their fig. 2) and found that four vertical zones are generally present. A basal stabilization stage (or zone) represents the initial preparation of the substrate for reef growth; in Palaeozoic reefs this typically involved the accumulation of small, localized mounds of echinoderm calcarenite. Reef-building organisms then preferentially colonized the early, stabilized mounds and a framework was gradually built up. In both the colonization and diversification stages there is a marked increase in the numbers and variety of both reef-building and reef-dwelling taxa. Implicit in this analysis is the assumption that each stage 'prepares the ground' for the succeeding stage. The various organisms of each stage grow and develop, and collectively alter the environment in such a way that in time they will be replaced by others more suited to exploit the newly created habitats. This is the classic autogenic succession of Tansley (1935). In the final stage, or domination zone, one or a few taxa predominate. The change from the diversification to domination zones is often abrupt and it may be that the latter represents the sudden imposition of allogenic (i.e. external) factors such as water turbulence.

Walker and Alberstadt (1975) are in no doubt that the stages in their analysis are interconnected and part of an irrevocable process of community development. They state (1975, p. 243; see also their fig. 1) that during the first three stages there is a steady increase in the following community parameters: the number of species, growth habit diversity, stratification, food-web complexity, and other organism interrelations. These increases lead to 'homeostasy by diversification' and result in the development of highly biologically accommodated assemblages.

Thus we arrive at a mechanism of fossil reef succession that may be termed 'community controlled'. The physical environment is progressively modified by the reef community to produce an orderly and, to some extent, predictable sequence of species. Reef biomass and diversity gradually increase and in time a stabilized, highly integrated community is produced. This mechanism seems to correlate well with many observed fossil reef successions.

SOME THEORETICAL CONSIDERATIONS

The community-control concept has had a profound influence on the study of ecological succession. Originating with works of Clements (1916, 1936), the idea of succession as an orderly process of community development has pervaded ecological thinking ever since (see, e.g., Olson 1958; MacArthur and Connell 1966; Margalef 1968; Odum 1969; and Whittaker 1975). However, appealing as this community-control theory may be, it must be pointed out that it is based as much on inference and analogy as it is on fact and observation. Few studies to date have actually documented an orderly replacement of early successional species by members of later communities (Drury and Nisbet 1973; Connell and Slatyer 1977). It has also been shown that the theory runs contrary to the principle of natural selection. If an early species 'prepares the ground' for a later one, it will be actively creating an environment that is more favourable to the survival of another species than to itself. Natural selection must act on all species including successional ones (Colinvaux 1973; Drury and Nisbet 1973). Much of the evidence for the progressive development of stabilized, highly integrated communities can in fact be shown to be no more than the result of the passage of time.

Biomass increases through succession because it takes time to grow, and diversity must progressively increase because a succession will always start with zero species. Far from representing a homeostatic equilibrium, the end point of succession may simply be the running-out of available species (Gleason 1926).

It has long been recognized (see, e.g., Egler 1954) that nearly all species in a successional sequence are either present before the sequence starts or appear shortly afterwards. Ecological succession may in fact be no more than a sequential expression of conspicuousness (Drury and Nisbet 1973, p. 352). Those species appearing early in a succession are simply those that are common and well dispersed, whereas those appearing later are less common and have slower mechanisms of dispersal. In time, progressively rarer species should colonize any given area (see, e.g., Gleason 1926; MacArthur and Wilson 1967; Goulden 1969).

This recognition of ecological succession as a sequential expression of conspicuousness represents a fundamental shift in emphasis from a consideration of properties of the community as a whole to those of the individual. Modern successional theory is now based on the fundamental roles of physical stress on individuals and competition between individuals for available resources (Colinvaux 1973; Drury and Nisbet 1973; Horn 1974, 1975, 1976). It is important for early successional species to be able to invade openings, grow, and mature quickly. For a time these early species will be able to suppress competitors, but they will be replaced eventually by later colonists that live longer and grow to greater sizes. This replacement of early colonists with 'opportunistic' strategies by later ones with 'equilibrium' strategies is well documented (Colinvaux 1973; Drury and Nisbet 1973; Horn 1974). It is analogous to MacArthur and Wilson's (1967) replacement of '**r** selected' species by '**K** selected' ones (see Odum 1969; Colinvaux 1973).

In an important review of successional mechanisms, Connell and Slatyer (1977) have stressed that the interactions of plants (or sessile animals) with herbivores, predators, and pathogens can also be of critical importance to the course of succession. Connell and Slatyer propose three simple models. The facilitation model is equivalent to that of community-control outlined above. It assumes that only certain early successional species can colonize a particular site. These then grow and modify the environment so that it is more suitable for colonization by later successional species. In the second and third models (the tolerance and inhibition models, respectively) any species, including those typical of late succession, may be able to colonize an area. The tolerance model is essentially similar to the mechanism of sequential conspicuousness in that later species are simply late arrivals or those that took longer to grow. They are tolerant species adapted to grow at lower levels of resources than early successional species. The work of Loucks (1970) suggested that the tolerance model may have widespread application, but Connell and Slatyer (1977) could find little evidence to support it.

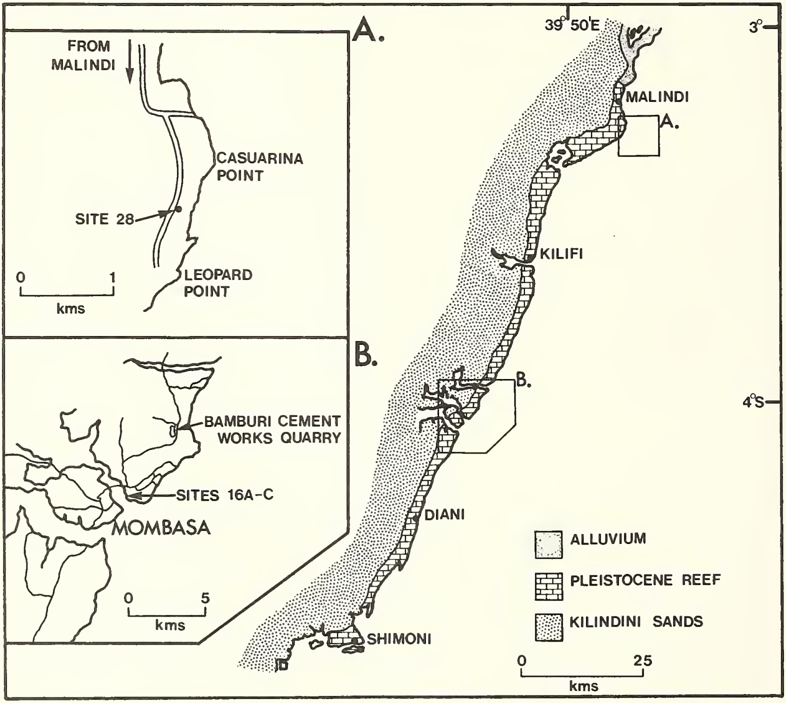
In the third (inhibition) model there are no faunal replacements until damage (by physical disturbances, predation, etc.) creates an opening in the community. Any available species can then invade the opening; there is no need for the ground to be prepared or for the replacing species to be more tolerant. As early successional species are by nature shorter-lived ones, they will in time gradually be replaced by the longer-lived late successional species. Ecological successions from short-lived to long-lived species are commonly observed (Connell and Slatyer 1977). An important point to note here is that, in the facilitation and tolerance models, species are progressively eliminated through competition, but in the inhibition model they are eliminated by the action of physical disturbances, herbivores, predators, and pathogens.

We may conclude from this brief review that more emphasis should be placed on elucidating the role of individuals in ecological successions. Geologists in particular should concentrate less on establishing vertical zones or stages and more on examining individual species. Detailed analysis of species abundance and distribution patterns at successive levels through a reef should reveal much about colonization strategies, relative growth rates, and competitive interactions. Direct evidence of interspecific interference and overgrowths may also be found, and in time it should be possible to establish the successional roles of the principal frame-building organisms in any reef tract. Only then will it be possible to test adequately models such as those outlined above.

Finally, it is important to bear in mind that most recent successional theories relate to the re-establishment of a pre-existing community in a relatively constant environment. In other words they deal with what are essentially secondary successions. On the other hand, many reef successions are concerned with the establishment of a new community (often in an inconstant environment) and as such are primary successions. Important differences can be expected between primary and secondary successional mechanisms.

FIELD AREA AND METHODS

The Pleistocene reef forms a narrow but continuous strip along the Kenya coast between Malindi and Shimoni (text-fig. 1). Uniform, unfossiliferous sands (the Kilindini Sands) are continuously exposed along its inner margin and there is evidence, especially in the Mombasa region, that these sands underlie (and thus pre-date) the main reef deposits. Whereas much of the early Pleistocene



TEXT-FIG. 1. A simplified geological map of the Kenya coast. Insets A and B show the locations of Sites 28 and 16A–C, respectively. The sites studied at the northern end of the Bamburi Cement Works quarry are shown in text-fig. 3.

history of the Kenya coast was dominated by the accumulation of sands (mainly of continental origin) on a low coastal plain, much of the later history was dominated by periods of reef growth. Detailed mapping along various parts of the coast has shown the reef stratigraphy to be complex, and as yet no precise chronology of reef-building events can be established. It is thought likely that the majority of exposures can be referred to a single (though complex) depositional event which took place during the last Interglacial (*c.* 120 000 years BP) (Crame 1977). However, limited exposures of lower reef limestone units occur in a number of areas, most noticeably Bamburi (text-figs. 1 and 2) and between Diani and Shimoni (text-fig. 1). In the Mombasa area the main reef limestones are 6–8 m thick. They thicken eastwards to form cliffs of 10–12 m, and thin westwards to 2–3 m at the junction with the Kilindini Sands (text-fig. 1).

It is also as yet impossible to present a detailed facies model of the Pleistocene reef, owing to uncertainty as to the contemporaneity of the various depositional units and lack of information in certain key areas. Enough is known, however, from those reconstructions that have so far been made (Crame 1977), to speculate on the general form of the reef.

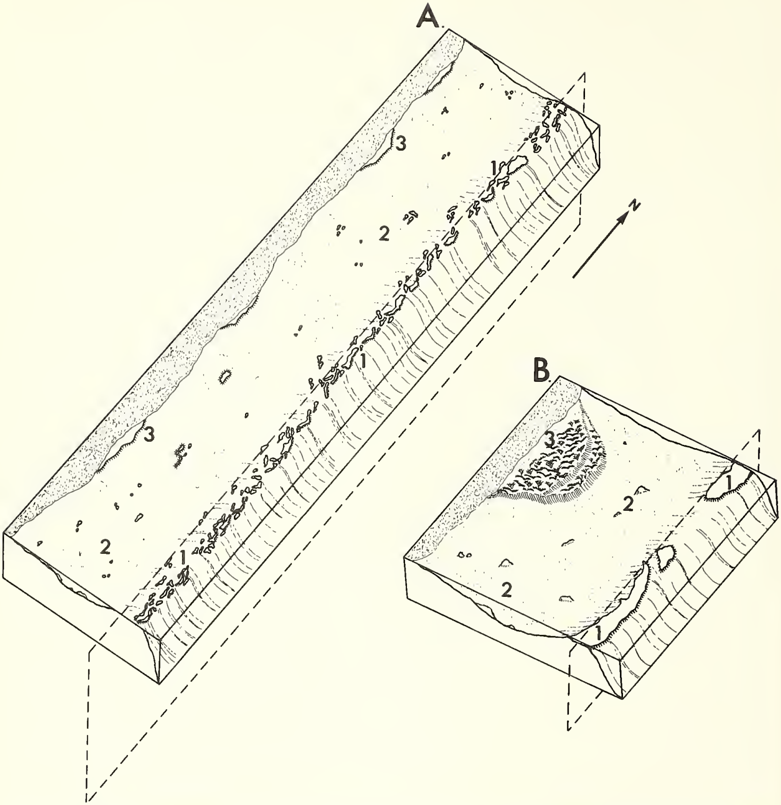
The present-day reef platform along the Kenya coast is primarily an erosional feature (pers. obs.; see also Crossland 1902, 1903), and what was the outer half of the Pleistocene reef has now been largely removed by marine erosion. Remnants of the seaward extremities are preserved, however, in certain headlands and creek mouths and these are typically composed of thick, branching *Acropora* assemblages. This outer *Acropora* facies probably represents the remnants of a series of small, isolated, and coalescing reef masses that developed along the reef margin close to the shelf edge (text-fig. 2A). Under constant wave attack, these outer reefs would have been dominated by thick algal crusts and shallow-water, high-energy *Pocillopora* and *Acropora* assemblages.

There is little extensive frame growth over much of the inner half of the Pleistocene reef, and it is clear that this was essentially a back-reef region supporting only small reef clumps and isolated coral mounds (text-fig. 2). Occasionally, however, larger reefs were able to develop in this back-reef region, perhaps opposite the more substantial gaps in the outer reef cluster. The *Acropora* bank exposed in the north and west faces of the Bamburi Portland Cement Works quarry may well be one such reef (text-figs. 1 and 2B).

Vertical sections through the Kenya Pleistocene reef can be studied in a series of quarries, road-cuts, and cliff-lines from Malindi to Shimoni (text-fig. 1). Over forty such sections have now been examined in detail as part of a long-term project to investigate the internal structure and development of a major reef tract. From these, a series of sections through dense coral framework was selected for an analysis of reef development in terms of ecological succession. In making this selection, an effort was made to choose sites that reflected reef growth in a variety of environments.

Sedimentary and faunal evidence suggests that all the areas of frame coral growth described in this work accumulated under conditions of relatively constant water depth. Bedding planes are rare in the surrounding matrix calcarenites, and there are no distinct horizons of either stunted or flat-topped coral colonies to suggest the sudden imposition of very shallow-water conditions. There is some evidence of a terminal shallow-water event in the Pleistocene reef limestones along some parts of the Kenya coast, but this occurs at a level well above the top of any of the sites studied.

Vertical quadrats, varying between 5 and 35 m in width and between 2 and 5 m in height, were marked out on each of the sections studied. A detailed map was then drawn, at a scale of 1 : 10, of each quadrat, and particular attention was paid to determining the shape and attitude of individual coral colonies. To this end, hachuring and shading were employed, and the resulting sketch of each section is in fact a three-dimensional picture. This method is of course more time consuming than merely plotting colony outlines or using symbols, but it was found to expedite greatly the subsequent analysis of the stages of reef development. Other features marked on the maps include minor sedimentary structures and patches of rubble. During construction of some of the maps, a number of loose coral colonies were encountered. If it seemed likely that a loose coral had grown in close proximity to where it now lay and had merely toppled over from its life position, it was included in the map and subsequent analysis. If, however, a coral showed signs of severe abrasion and had obviously been transported, it was regarded as reef rubble and excluded from the analysis.



TEXT-FIG. 2. A three-dimensional model of the Kenya reef during the last Interglacial. A. The reef tract between Malindi and Shimoni. 1. Outer reef wall: composed of isolated and coalescing reef masses. 2. Back-reef region: predominantly small, isolated coral mounds and patches. 3. Small fringing reefs: developed at intervals along the sandy shore. B. A generalized reconstruction of the reef in the region of the Bamburi Portland Cement Works quarry. 1. Outer reef wall. 2. Back-reef region: scattered coral mounds on a sandy-calcarenite substrate. 3. An *Acropora*-dominated bank. In both A and B the portion of the block lying to the right of the dashed rectangle has now been removed by marine erosion. The width of both blocks is approximately 5 km.

Very few corals fell into the latter category. Wherever possible, the base of a quadrat was placed on or close to a stratigraphic break, to investigate the pioneer coral faunas that had colonized bare surfaces. A particularly useful datum to use in this context is the top of the underlying sands formation.

The resulting maps were analysed at half-metre vertical intervals. Numbers of coral species and individuals were determined for each interval, and an estimate made of individual coral colony size. For the latter, the outline of the colony, as projected onto the plane of the paper, was taken to represent a vertical section through it. The area of this outline was then calculated using a simple grid-overlay technique. The resulting figure, the number of squares on the grid occupied by a planar section through the colony, has been termed the Importance Value of the coral. The species diversity of each half-metre interval was calculated using the Shannon–Weaver information theory index:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

(where H' is the information content of the sample, S is the total number of species, and p_i is the proportion of the total sample belonging to the i^{th} species). It should be noted that the validity of using an information theory index such as this to measure biological diversity has been seriously questioned (see, e.g., Hurlbert 1971; Horn 1974; Goodman 1975; May 1975). However, of all the various measurements that incorporate the relative abundances of species, the Shannon–Weaver is the one most widely used. It has been consistently employed in the study of recent coral assemblages (Loya 1972, 1976*c*; Porter 1972*a*, *b*; Grigg and Maragos 1974) and its continued usage is advocated here in the hope that it may eventually lead to a detailed comparison of coral species diversity patterns in a range of contrasting reef environments.

The function H' is influenced by both numbers of species in the sample (S) and the evenness of their distribution among the individuals in the sample (Lloyd and Ghelardi 1964). A greater number of species will increase the species diversity and so too will a more even (or equitable) distribution among the species. Equitability (J') can be measured in a number of ways (Pielou 1975), one of the simplest being:

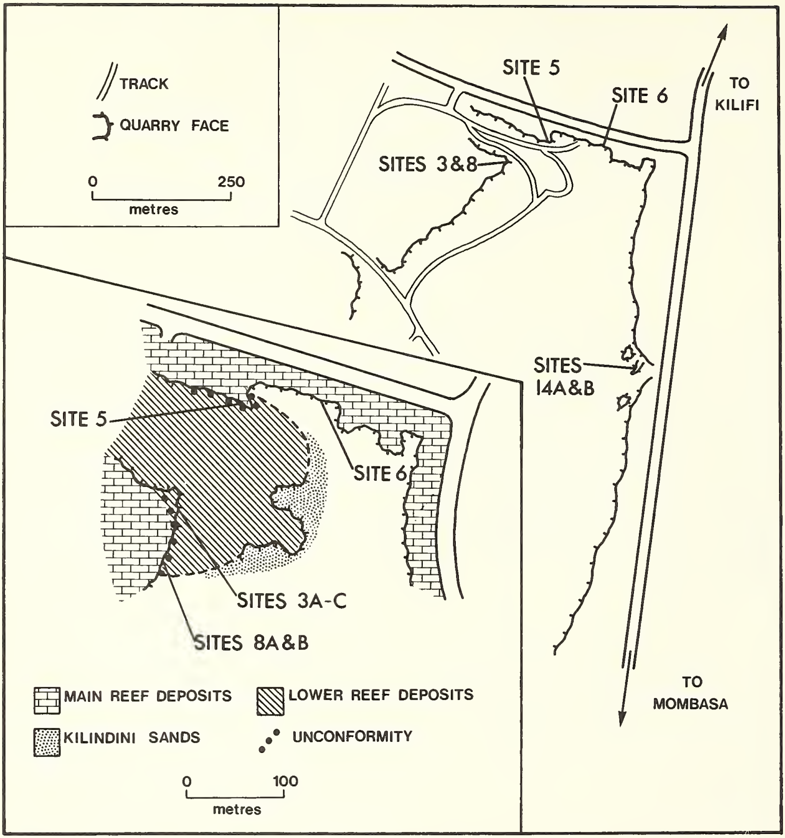
$$J' = \frac{H'}{H_{\max}}$$

(where $-H_{\max} = \log S$ is the maximum value of H', which occurs when all species in the sample are equally distributed among the individuals).

The degree of preservation of the corals is often such as to prevent accurate identification to the species level. In a number of instances the fine detail of calice structure and surface ornament has either been removed (by weathering or diagenetic solution) or obscured (by encrusting organisms or sediment). Consequently it has not been possible to identify certain types of coral beyond rather broadly defined groups. An explanation of the grouping used in this study is contained in the Appendix.

SUCCESSION ON SHALLOW-WATER, UNCONSOLIDATED SUBSTRATES

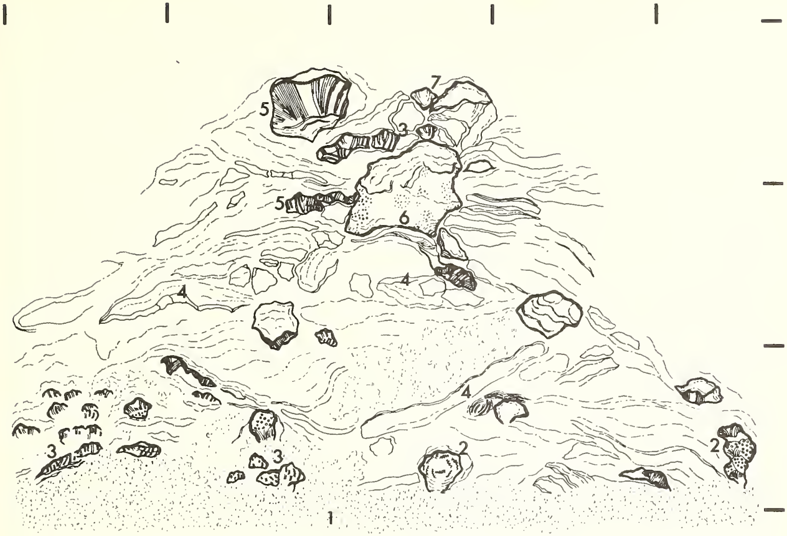
At the northern end of the Bamburi Portland Cement Works quarry, a lower series of reef deposits is separated from the main reef by a marked unconformity (text-fig. 3). These lower deposits developed directly on the lower sands formation in what were, at least initially, very shallow-water conditions. High angle cross-bedding, large quartzose pebbles, and patches of coarse coral-mollusc debris all occur along the line of the sands–reef transition zone and suggest that at times beach-type conditions prevailed. Directly above this transitional layer, low, irregular domes and patches of coral framework, measuring up to 2·5 m (horizontal) by 2 m (vertical), are developed. These framework areas alternate with comparatively barren patches of sandy calcarenite that support only small composite coral mounds and isolated coral colonies. Three quadrats were studied in this area



TEXT-FIG. 3. Sites studied at the northern end of the Bamburi Portland Cement Works quarry. The inset is a geological sketch-map showing the approximate distribution of the principal depositional units.

(Sites 3A, 3B, and 3C, text-fig. 3) through three separate framework structures. Sites 3B and 3C are adjacent and separated by 4 m of barren calcarenite from Site 3A. The base of the quadrat at all three sites was placed at the top of the sandy transitional layer, and it is believed that the structures described developed at approximately similar elevations above the sea floor.

Similar mounds of coral framework are exposed in cuttings along the Malindi–Leopard Point road (text-fig. 1, inset A). These mounds, although of similar height, have slightly greater linear dimensions and are set closer together. They contain some extremely high densities of corals, and



TEXT-FIG. 4. Part of the quadrat studied at Site 3A. *Key*: 1. lower sands formation, 2. early doming-massive faviids, 3. small clumps of *Galaxea fasicularis*, 4. thick, encrusting layers of matrix, 5. later faviids, 6. a large colony of *Favia stelligera*, 7. a small clump of *Acropora* and *Pocillopora*. Horizontal and vertical grid interval: 0·5 m.

altogether this would appear to have been an area of more prolific coral growth. The mounds developed on a sandy substrate, but their bases are nowhere clearly exposed. It is believed that they form part of the main reef limestones and thus post-date the reef deposits at Site 3.

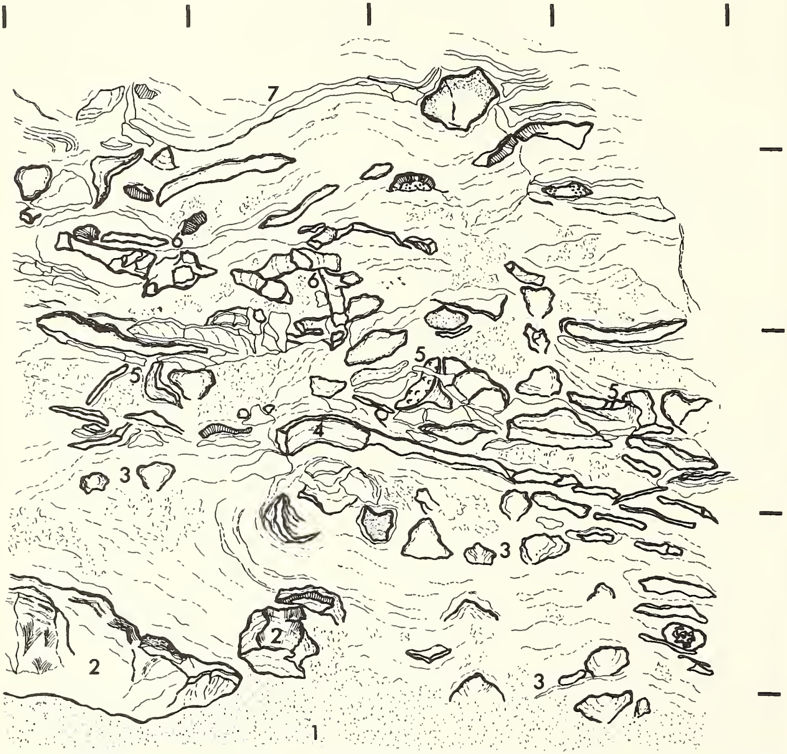
Succession at Site 3A (text-figs. 4 and 6) (quadrat size: 4 m (horizontal) × 1·5 m (vertical))

The most important initial colonizer on the sands at this site is *Galaxea fasicularis* (Lamarck). It occurs in small, spiky (fasiculate) clumps that are often totally encased in sandy matrix. Small doming-massive faviids also occur within the lowest half-metre (text-fig. 4) but there are virtually no branching types such as *Acropora* or *Pocillopora*. *G. fasicularis* is known to be a particularly efficient sediment-remover that thrives at the present day in shallow, sandy environments (Marshall and Orr 1931). In this particular instance, low mounds formed by the coalescing spiky clumps must have given important initial relief to the local reef structure (text-fig. 4).

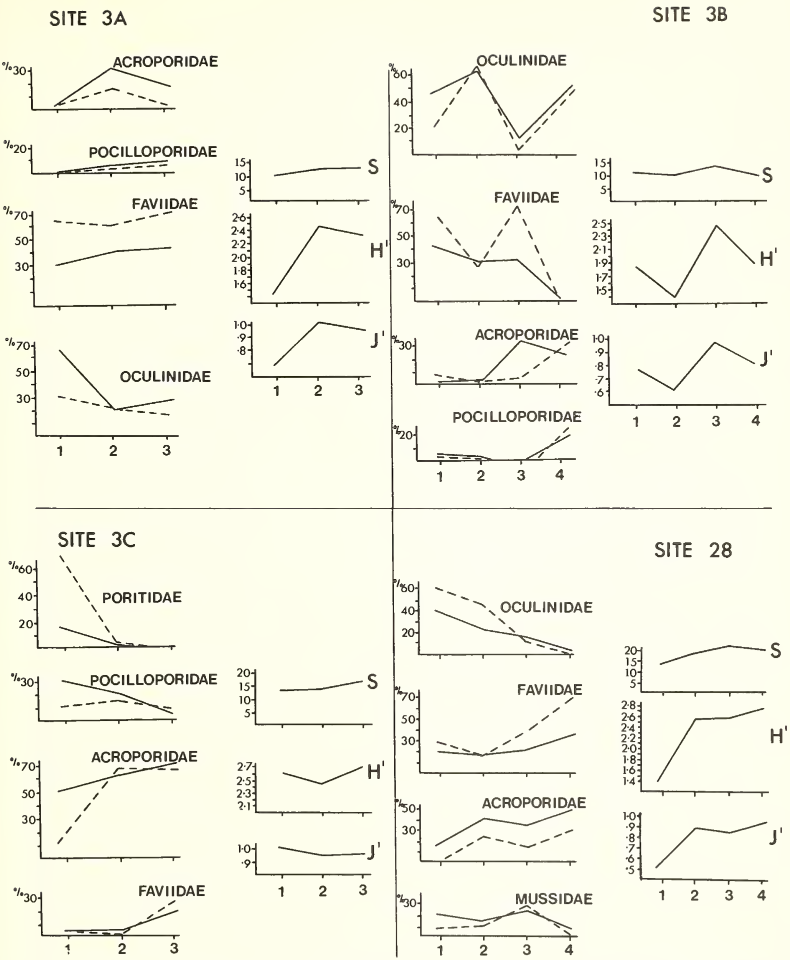
Also prominent in the first and second intervals are doming-massive faviids such as *Favia*, *Favites*, *Goniastrea*, and *Platygyra* (text-figs. 4 and 6). These are all robust types capable of withstanding the forces of shallow, turbulent seas (e.g. Wells 1954; Yonge 1973) and, by virtue of their large polyps, they are also efficient sediment-removers (e.g. Marshall and Orr 1931; Maxwell 1968; Mergner and Scheer 1974). The hillocky growth form of *Favia stelligera* (Dana) is typical of shallow, turbulent environments (Wells 1954; Wijsman-Best 1972, 1974) and large colonies such as that seen in the second interval of the quadrat (text-fig. 4) must have considerably promoted early topographic development of the reef. Associated with the increase in topographic complexity in the second and third intervals is the occurrence of a number of small branching corals belonging to the families Acroporidae and Pocilloporidae (text-figs. 4 and 6).

Succession at Site 3B (text-fig. 6) (2·5 × 2 m)

The vertical sequence in this quadrat is essentially similar to that seen at Site 3A. Low mounds formed by clumps of *Galaxea fasicularis* predominate in the first two intervals, together with doming-massive faviids (of which *Favia* sp. gp. 1 is particularly common). The graphs (text-fig. 6) document the progressive demise of these large-calice faviids and the rise of both the Acroporidae and



TEXT-FIG. 5. The quadrat studied at Site 3C. *Key*: 1. lower sands formation, 2. massive *Porites*, 3. small clumps of *Pocillopora*, 4. thick, platy *Acropora*, 5. mixed *Acropora–Pavona* assemblage, 6. thick-branching *Acropora*, 7. layers of matrix. Horizontal and vertical grid interval: 0·5 m.



TEXT-FIG. 6. Coral trends and diversity trends for Sites 3A, 3B, 3C, and 28. The coral trends are given as percentages of the total coral fauna occupied by the principal Families at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (*S*), the Shannon–Weaver information index (*H′*), and Pielou's measure of equitability (*J′*). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat.

Pocilloporidae in the later stages. It would appear that, once a certain elevation had been attained, species of both *Acropora* and *Pocillopora* were able to colonize the area. The trends for *G. fasicularis* (Oculinidae, text-fig. 6) show pronounced fluctuations.

Succession at Site 3C (text-figs. 5 and 6) (2 × 1·5 m)

In marked contrast to Sites 3A and 3B, the initial coral assemblage developed on the sands at this site is composed of small clumps of *Pocillopora* and several large colonies of massive *Porites* (text-fig. 5). However, small, bushy species of *Pocillopora*, similar to those seen here, are known to thrive in environmentally unpredictable areas such as reef flats (e.g. Mayor 1924; Crossland 1928; Manton 1935), and Marshall and Orr (1931) have shown that *P. bulbosa* (? = *P. damicornis* (Linnaeus)), like *G. fasicularis*, is capable of withstanding large influxes of sediment. Species of massive *Porites* are hardy too, and in many parts of the Indo-Pacific province have been observed to colonize soft (generally sandy) substrates (e.g. Manton 1935; Umbgrove 1947; Maxwell 1968; Maragos 1974*a*).

The early *Pocillopora–Porites* assemblage is replaced in the second and third intervals by a thick framework of branching, encrusting, and doming-massive corals (text-fig. 5). Species of *Acropora*, especially *A. palifera* gp. 1, *A. palifera* gp. 3, and *Acropora* sp. gp. 8, predominate, together with several thick-branching colonies of *Pavona clavus* (Dana) and the occasional massive faviid. Both the Poritidae and the Pocilloporidae decrease in importance up the quadrat, as the Acroporidae and Faviidae increase (text-figs. 5 and 6).

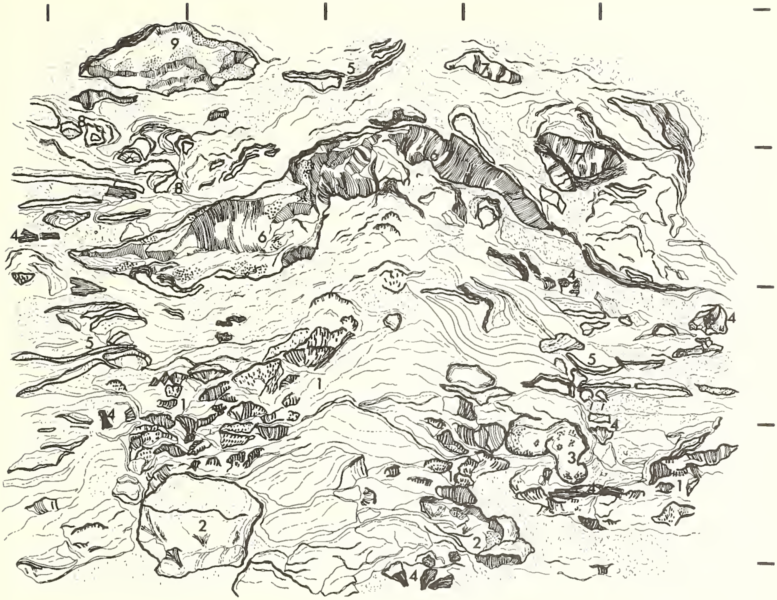
Diversity trends through succession at Sites 3A, 3B, and 3C

There is obviously no progressive increase in species diversity through succession at these three sites (*H′* values, text-fig. 6). At various levels all three quadrats show pronounced drops in diversity and it would seem that this is largely due to the dominance exerted by certain coral species. When resources (especially available habitat space) become limiting, fewer species will be able to coexist and the competitively successful ones, such as the faster-growing types, will become dominants. Grigg and Maragos (1974) have suggested that dominance in coral faunas is brought about by competitive interactions such as exploitation or pre-emption (i.e. rapid growth), interference, or predation (see Lang 1971, 1973). It is probable that large faviids exerted a dominant influence in the third interval at Site 3A, *G. fasicularis* in the second and fourth intervals at Site 3B, and large species of *Acropora* in the second interval at Site 3C. Concomitant with the rise of these dominants there is in each case a marked fall in diversity.

It might be expected that the evolution of dominance will affect the equitability component of species diversity rather more than the species richness component. Under normal circumstances the general trend for a *J′* curve should be a progressive increase through succession as the individuals present become more evenly distributed among the various species. A sudden influx of individuals, however, associated with the rise of a dominant species, would seriously disrupt this process and cause a sharp fall in *J′* values. It is indeed the case that at all three sites the form of the *J′* curve closely resembles that of the *H′* curve (text-fig. 6).

Succession at Site 28 (text-figs. 1, 6, and 7) (5 × 2 m)

The quadrat at this site was positioned in the centre of a low mound measuring just over 10 m across and ranging in height from 2·5 m in the centre to 1 m at either end. The lowest interval of the quadrat is dominated by thick intergrowths of *G. fasicularis* and large doming-massive faviids (principally *Platygyra* sp. and *Favia* sp. gp. 1) (text-fig. 7), and again there is evidence that these coral types flourished in a shallow, sandy environment. The mussid, *Lobophyllia*, and a few small colonies of platy *Acropora* are the only other corals present in the first interval (text-figs. 6 and 7). In the middle and upper levels of the second interval there is an abrupt change to a rich *Acropora*—faviid assemblage (text-fig. 7). Within this assemblage there are platy and branching acroporids (*Acropora* sp. gps. 2, 3, 6, and 7), doming-massive and encrusting faviids (*Favia*, *Platygyra*,



TEXT-FIG. 7. Part of the quadrat studied at Site 28. *Key*: 1. dense clumps of *Galaxea fasicularis*, 2. *Platygyra* sp., 3. *Favia* sp. gp. 1, 4. *Lobophyllia*, 5, platy-encrusting *Acropora*, 6. *Diploastrea heliopora*, 7. *Leptoria phrygia*, 8. mixed *Acropora* assemblage, 9. *Leptastrea* sp. gp. 2. Horizontal and vertical grid interval: 0·5 m.

Goniastrea, *Hydnophora*, and *Echinopora*), and a few scattered colonies of *Galaxea* and *Lobophyllia*.

Diversity rose abruptly upon establishment of the initial mound but then rose more gradually through the rest of the quadrat (*H′* values, text-fig. 6). Clearly, the *Galaxea*–faviid assemblage provided a topographic prominence that was subsequently colonized by a wide variety of other coral types.

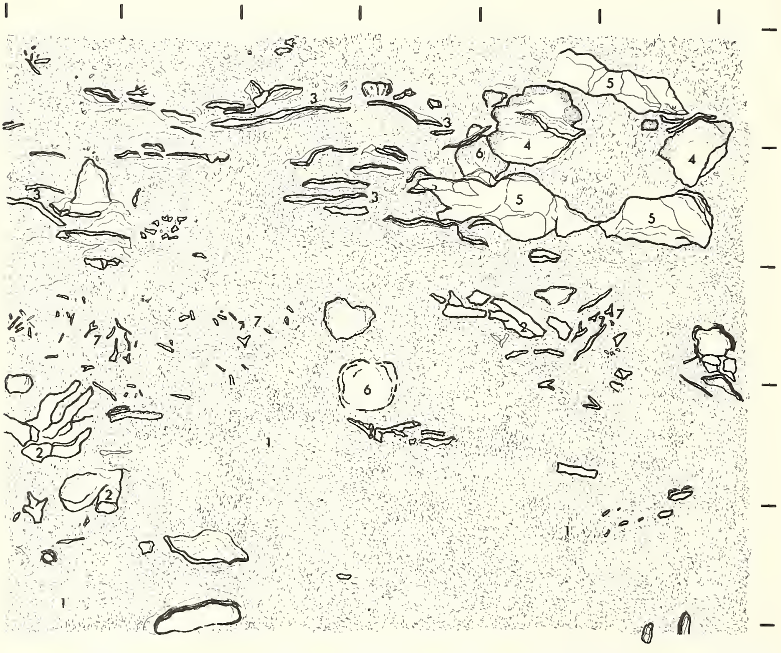
This vertical sequence is very similar to that seen at Sites 3A and 3B. That a more substantial coral assemblage subsequently developed on the *Galaxea*–faviid base at this site suggests that there were subsequently slightly deeper or calmer-water conditions in this area.

SUCCESSION ON DEEPER-WATER, UNCONSOLIDATED SUBSTRATES

Quadrats studied at two sites in the Bamburi Portland Cement Works quarry (Sites 6 and 14, text-fig. 3) record the establishment and subsequent development of coral assemblages on soft substrates in deeper-water environments (the estimated depth at both sites being in the 10–30 m range).

The coral assemblage at Site 6 is dominated by two distinctive elements: large platy colonies of *Acropora* which have shallow, saucer-shapes in cross-section, and are often stacked in tiers, and thick-branching clumps of *A. palifera* (= *A. palifera* gp. 1). It closely resembles reef front terrace assemblages developed at depths of about 10 m on both the Great Barrier Reef (e.g. Maxwell 1968, fig. 77) and Tutia Reef, Tanzania (Talbot 1965).

Immediately to the north and east of the second site (Site 14, text-fig. 3), patches of a plain, uniform calcarenite are exposed that contain no corals other than the tiny ahermatypic forms *Heteropsammia* and *Heterocyathus*. Both of these occur at the present day on sheltered, sandy bottoms at depths generally between 10 and 30 m (Goreau and Yonge 1968; Wijsman-Best 1972; Rosen 1972; Pichon 1974). At Site 14 itself, however, a rich assemblage of corals is exposed in a complex knoll measuring some 15–20 m across in its longest dimension and 2·5–3 m in height in the centre. The quadrat at Site 14A is oriented in an approximately north–south direction through the knoll, and that at Site 14B in an east–west direction. The two quadrats are separated by a horizontal distance of 5 m. It is believed that similar-sized knolls developed sporadically in the region of what is now the eastern margin of the Bamburi Portland Cement Works quarry, together with large, isolated coral colonies (among which *Porites* sp. gp. 2 are common). These knolls and corals grew up from what was essentially a level, sandy bottom.

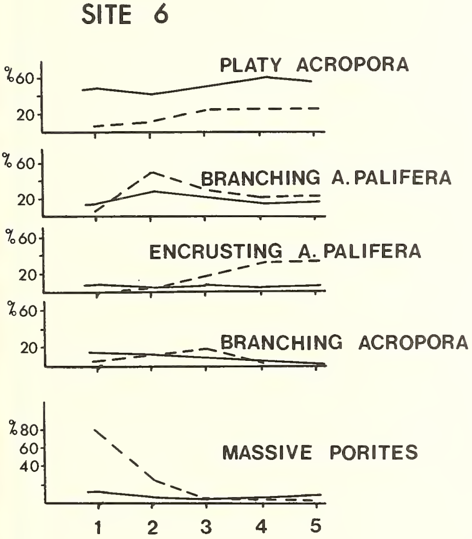


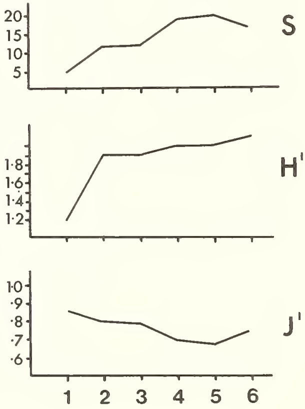
TEXT-FIG. 8. Part of the quadrat studied at Site 6. *Key*: 1. sparsely populated *Halimeda* calcarenite, 2. thick-branching *Acropora palifera*, 3. platy *Acropora*, 4. massive *Porites*, 5. massive-encrusting *A. palifera*, 6. *Pocillopora* sp., 7. branching rubble. Horizontal and vertical interval: 0·5 m.

The deposits at Sites 6 and 14 are part of the main reef limestones and are thought to rest directly on the lower Kilindini Sands unit. They represent deeper-water facies that developed along the northern and eastern flanks of the Bamburi quarry, respectively. Contemporaneously, shallower-water *Acropora*-dominated assemblages developed in the region of the western margin of the quarry (Crame 1977, fig. 38).

Succession at Site 6 (text-figs. 8 and 9) (25 × 2·5 m)

The vertical sequence revealed in the quadrat at this site is rather different from those previously described. Corals are less abundant, there are no extensive areas of frame, and no dramatic faunal replacements occur (text-figs. 8 and 9). Species of *Acropora* predominate, and the principal coral elements, platy *Acropora* species and thick-branching *A. palifera*, remain relatively constant (at least in terms of numbers of colonies present) throughout the quadrat. There is, however, a gradual increase in both coral abundance and diversity (text-figs. 8 and 9). In the three highest intervals further species of *Acropora* are encountered, together with occasional colonies of types such as *Pocillopora* sp., *Porites* sp. gp. 1, *Porites* sp. gp. 2, and a few small faviids. The process of ecological succession at this site has clearly been one of the very gradual colonization of a barren substrate, followed by an incremental build-up of both coral species abundance and diversity.





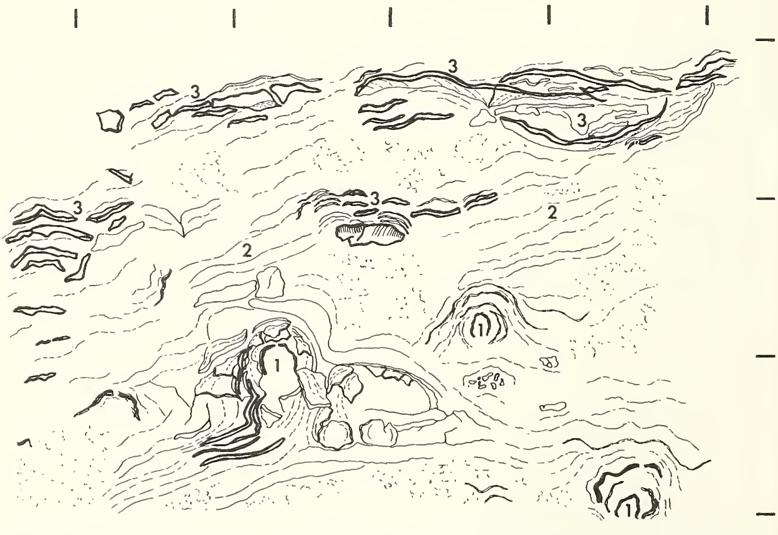
TEXT-FIG. 9. Coral trends and diversity trends for Site 6. The coral trends are given as percentages of the total coral fauna occupied by the principal coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (S), the Shannon–Weaver information index (H'), and Pielou's measure of equitability (J'). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat.

After a sharp initial rise, the H' curve then increases only comparatively slowly through the rest of the quadrat (text-fig. 9). It will be noted too, from text-fig. 9, that whereas the species richness (S) curve increases from the first to the fifth interval, the equitability curve (J') steadily decreases. The reason for this is that, in the early stages of succession, the addition of further species (i.e. increasing the species richness, S) has the effect of increasing the diversity value H' for the whole assemblage. At later stages, however, the addition of further species tends to decrease the value of H', since these later arrivals are rarer in occurrence and will thus upset the equitability (J'). The net effect of these two trends is to produce an H' curve that increases sharply initially but then levels off (text-fig. 9; compare also Loya 1972, fig. 9). In the sixth interval the S values fall for the first time and the J' values rise. This probably marks the end of species immigration into the area and the establishment, for the first time, of an equilibrium assemblage.

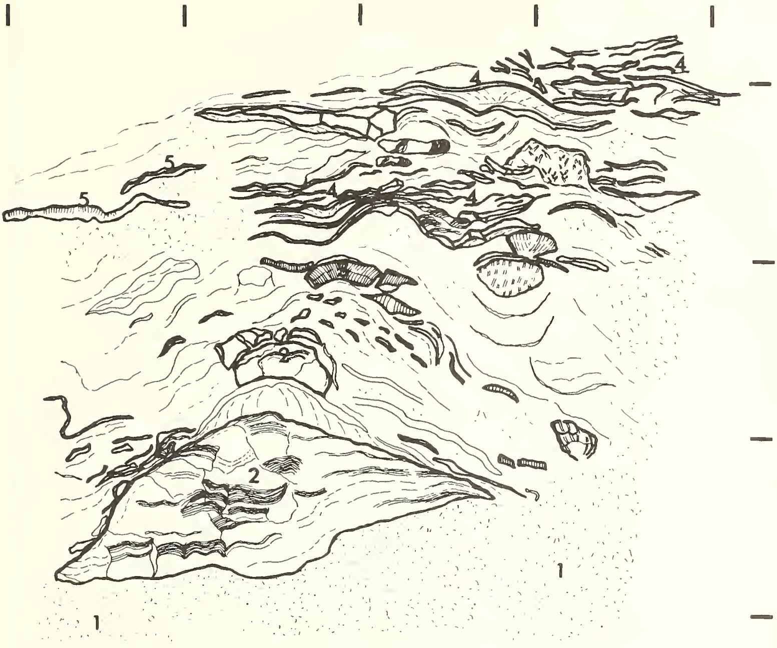
Succession at Site 14 (text-figs. 10 and 11) (14A: 5 × 1·5 m) (14B: 2·5 × 1·5 m)

Conspicuous at the base of the quadrat at Site 14A are a number of small, ball-like structures (text-fig. 10). These are in fact small coral colonies that have been coated with thick layers of encrusting algae and coral. Coral cores within the structures include small, massive heads of *Porites* sp. gp. 2, *Favia* sp. gp. 1, and *Platygyra* sp., and doming-encrusting *Montipora* sp. Later encrusting corals are predominantly *Pachyseris* sp. and *Montipora* sp.

In the second and third intervals the ball structures are replaced by thick layers of sediment and thinner platy-encrusting layers of coral (text-fig. 10). At this particular site *Montipora* sp. is the commonest of these later platy corals, but there are also a few small colonies of *Pachyseris* sp. It



TEXT-FIG. 10. Part of the quadrat studied at Site 14A. *Key*: 1. coral domes covered with layers of encrusting algae and coral, 2. platy layers of sediment, 3. layers of platy-encrusting coral, mostly *Montipora* sp. Horizontal and vertical grid interval: 0·5 m.



TEXT-FIG. 11. The quadrat studied at Site 14B. *Key*: 1. plain calcarenite, 2. massive *Porites*, 3. encrusting *Goniastrea pectinata*, 4. *Pachyseris* sp., 5. platy *Montipora* sp. Horizontal and vertical grid interval: 0·5 m.

would thus appear that the early ball-like structures formed an initial protruberance on the sea floor that was subsequently covered by thick, platy layers of sediment and coral.

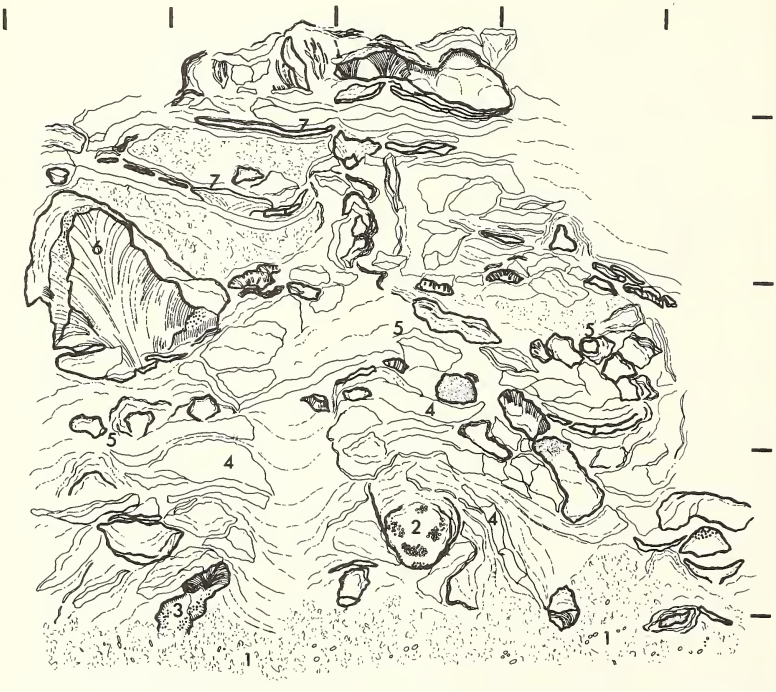
At Site 14B the initial relief was provided by a single, large, doming-massive colony of *Porites* sp. gp. 2, which grew directly on the fine calcarenite substrate (text-fig. 11). Later corals, including another massive *Porites* and a thick, doming-encrusting *Goniastrea pectinata* (Ehrenberg), accentuated the initial dome formed by the *Porites* and a distinct hummock must have been produced on the sea floor. This feature was subsequently covered by a succession of platy-encrusting coral layers (principally *Pachyseris* sp.) (text-fig. 11).

As light intensity decreases with depth on a reef, so competition must increase among corals to occupy space in the light. A good strategy for such competing corals is to have a high surface to volume ratio (i.e. to be platy or sheet-like in form; e.g. Goreau 1963; Barnes 1973). Unfortunately, a reef structure cannot be built entirely out of platy corals for they would be unable to lift it significantly above the sea floor and it would have little intrinsic strength. It is suggested that the successions seen at Sites 14A and 14B are, in essence, the sequence by which any deeper-water knoll reef might be expected to develop. Initially, a solid foundation is formed, and then, when sufficient relief has been developed, the mound is colonized by platy corals.

Quantitative analysis of the faunal trends was not possible at Sites 14A and 14B as many of the platy corals are too thin for the areas of vertical sections through them to be accurately measured. In many instances too, it is impossible to determine the number of separate colonies that are present.

SUCCESSION ON HARD SUBSTRATES

The prominent unconformity between the main-reef and the lower-reef deposits at the northern end of the Bamburi Portland Cement Works quarry (text-fig. 3) is subaerial in origin. This means that the early part of the main reef in this area developed on a hard substrate, in marked contrast to almost all the other areas investigated. The unconformity is well exposed at Site 8 (text-fig. 3), where immediately above it there is a thin, sandy-rubbly layer containing both coral fragments and iron-stained quartz pebbles. Two quadrats with their bases resting directly on this transitional layer were studied at Site 8. They are separated by a horizontal distance of 2 m and it is believed that



TEXT-FIG. 12. The quadrat studied at Site 8A. *Key*: 1. transitional sandy-rubbly layer, 2. doming *Favia* sp. gp. 1, 3. doming *Goniastrea retiformis*, 4. layers of matrix, 5. mixed *Acropora–Pocillopora–Porites* assemblage, 6. a later-colonizing *Astreopora horizontalis*, 7. platy *Acropora*. Horizontal and vertical grid interval: 0·5 m.

the structures described within them developed synchronously and to similar levels above the substrate. A third quadrat studied at Site 5 (text-fig. 3) has its base at an estimated height of 1–1·5 m above the sandy transitional layer. It is judged that the structure described within this quadrat attained similar dimensions to those at Sites 8A and 8B, but that it occupied a slightly higher position on the gently sloping eroded surface of the Lower Reef Series. The main reef in the vicinity of both Sites 5 and 8 is predominantly an *Acropora* facies (Crame 1977, fig. 38), with small branching and platy-based *Acropora* colonies being especially prominent.

Succession at Site 8A (text-figs. 12 and 14) (2·5 × 1·5 m)

At the base of this quadrat there are two small but prominent mounds, each of which is cored by a doming-massive faviid (one is *Favia* sp. gp. 1, the other *Goniastrea retiformis* (Lamarck)) (text-fig. 12). As before, it is thought that these were probably tolerant corals able to thrive in a high-energy, sand-transporting environment. They would be both resistant to strong water movements and capable of removing considerable sediment influxes. On recent reefs, both *G. retiformis* and many large-calice species of *Favia* frequently adopt such pioneering roles in shallow, sandy environments (e.g. Mergner and Scheer 1974; Maragos 1974*a*; Wijsman-Best 1974).

Thick layers of sandy matrix eventually encased the two early colonizing doming-massive corals (text-fig. 12) to form a low but distinct mound. This feature was subsequently colonized by a variety of corals, including *Pocillopora* sp., several species of branching *Acropora*, *Porites* sp. gps. 1 and 2, *Astreopora* sp., and *Galaxea fasicularis.* Fairly rapidly, however, *Acropora* species become dominant, and by the third interval they are by far the most important type (text-figs. 12 and 14). Corymbose species (predominantly *Acropora* sp. gp. 3) and small forms with platy bases (*Acropora* sp. gp. 7) are particularly common.

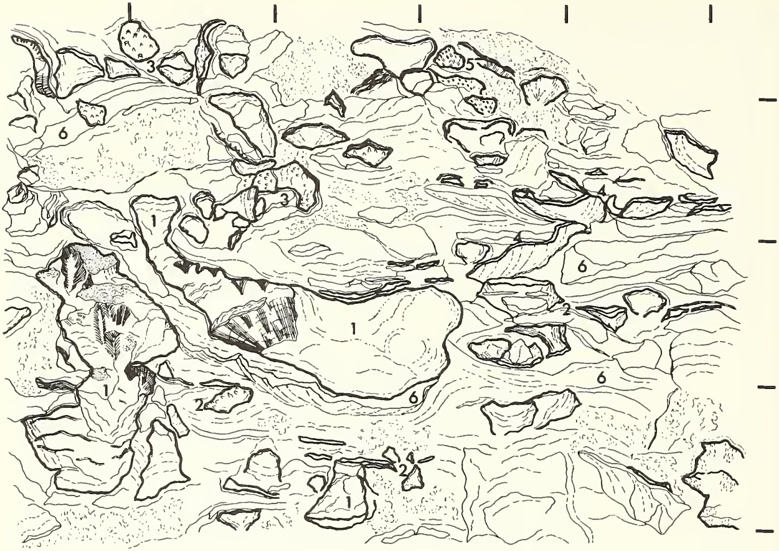
Succession at Site 8B (text-fig. 14) (2·5 × 1·5 m)

Three colonies at the base of this quadrat also have doming-massive forms, but are different species from those seen at the base of 8A. Two of the colonies are species of the caryophyllid genus, *Gyrosmilia*, and the third is *Porites* sp. gp. 2. Little is known about the habits of *Gyrosmilia*, but its large meandrine calices probably reflect an efficient sediment-clearing mechanism and this, together with its robust growth form, would make it a potentially good early colonizer of bare surfaces.

In this quadrat the pioneers are replaced even more dramatically by species of *Acropora* than at Site 8A. Small, branching colonies of *Acropora* dominate the second and third intervals, with corymbose species (*Acropora* sp. gps. 1–3) and horizontally branching sprays (*Acropora* sp. gp. 6) being especially common. The striking rise in the Acroporidae at the expense of all the other coral families is clearly illustrated in text-fig. 14.

Succession at Site 5 (text-figs. 13 and 14) (4 × 1·5 m)

The coral assemblage in the lower levels of the quadrat at this site is dominated by two distinctive elements: large, doming-massive colonies of *Porites* sp. gp. 2 and comparatively small colonies of branching *Acropora* (text-fig. 13). The latter include forms with distinct platy bases and some small sprays, but most characteristic are a number of corymbose colonies of *Acropora* sp. gps. 2 and 3. Towards the top of the second interval and in the third interval, however, there is a pronounced change. The coral fauna here is dominated by branching forms (with corymbose *Acropora* being especially common) and doming-massive forms are virtually absent (text-fig. 13). It would seem then, that after the early establishment of a mixed coral fauna, the branching corals, and in particular the relatively faster-growing species of *Acropora* (see, e.g., Stoddart 1969 for a summary of coral growth rates), replaced nearly all the other coral types and dominated the reef. *Acropora* sp. gps. 2 and 3 are the dominant species in the third interval (text-figs. 13 and 14), but there are also a few small colonies of types such as *A. palifera* (platy and encrusting forms), *Montipora*, *Porites* sp. gp. 1, and *Galaxea fasicularis.*



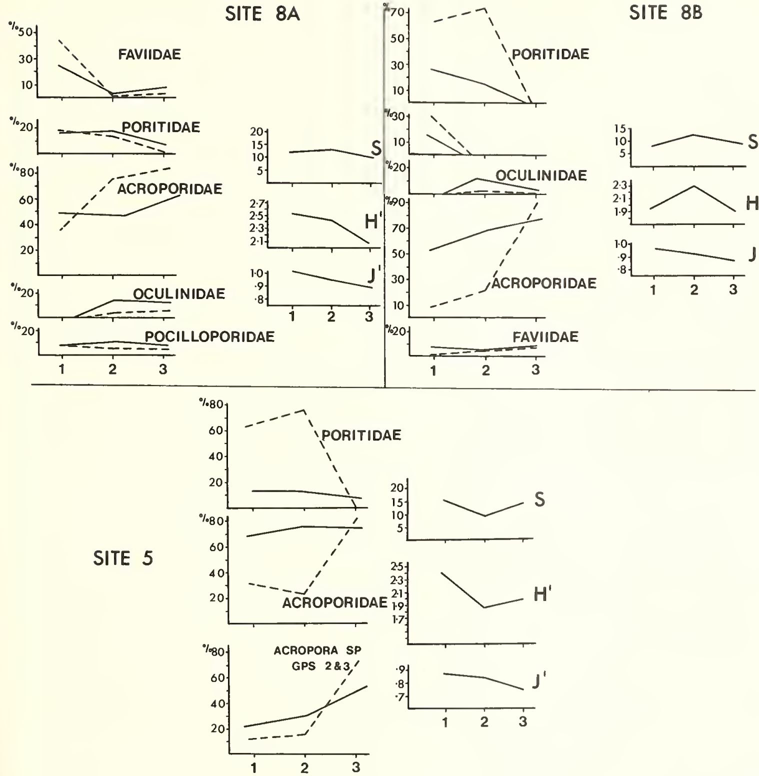
TEXT-FIG. 13. Part of the quadrat studied at Site 5. *Key*: 1. massive *Porites*, 2. mixed stands of *Acropora*, 3. dense clumps of corymbose *Acropora*, 4. platy *Acropora*, 5. *Galaxea fasicularis*, 6. layers of matrix. Horizontal and vertical grid interval: 0·5 m.

Both Gravier (1910) and Mayor (1924) suggested that the faster-growing corals, and in particular species of *Acropora*, would in time displace the doming-massive forms on a reef, and Connell (1973, 1976), by direct observation of fixed quadrat sites, has actually observed this process in operation. Indeed, were it not for the fact that many slower-growing species can protect themselves from being overgrown by extruding mesenterial filaments and killing off the encroaching edge of a competitor (Lang 1971, 1973; Connell 1976), competition would be much more rapid, and the very existence of numerous slow-growing shallow-water corals would be seriously jeopardized.

Diversity trends through succession at Sites 8A, 8B, and 5

The fall in diversity throughout the quadrat at Site 8A and the sharp drop from the second to the third interval at 8B (H' curves, text-fig. 14) almost certainly reflect the strong dominance exerted by species of *Acropora*. The trend at Site 5 is less easily explained in these terms, as the establishment of the dominant corymbose *Acropora* assemblage in the third interval is actually accompanied by an increase in diversity (H' curve, text-fig. 14). However, the diversity value obtained for the second interval is an extremely low one, as two very large *Porites* colonies occupy much of the available space (text-fig. 13). The progressive imposition of dominance is mirrored in the continual fall in J' values through succession at all three sites (text-fig. 14).

Sedimentary and faunal evidence suggests that shallow-water conditions (probably in the 2–10 m depth range) prevailed at both Sites 8 and 5. Once again, it would appear that the early evolution of dominance can be linked to reef initiation and development in a shallow-water environment.

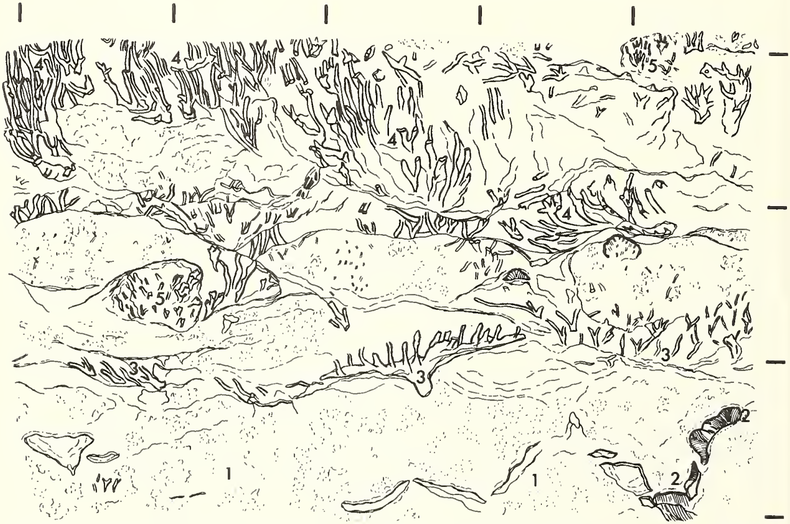


TEXT-FIG. 14. Coral trends and diversity trends for Sites 8A, 8B, and 5. The coral trends are given as percentages of the total coral fauna occupied by the principal Families and coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (*S*), the Shannon–Weaver information index (*H′*), and Pielou's measure of equitability (*J′*). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat. N.B. The trend for the Acroporidae at Site 8A is considerably influenced by the large later-colonizing *Astreopora*.

SUCCESSION IN A STAGSHORN *ACROPORA* AREA

Although stagshorn species of *Acropora* (= *Acropora* sp. gp. 4 in this study—see Appendix) are common constituents of many shallow-water coral assemblages, they are rather rare in the Kenya Pleistocene reef. However, a stagshorn-dominated assemblage is exposed near the mouth of the Nyali Creek in a 500 m strip of cliff-line along the eastern bank (Site 16, text-fig. 1). Here, a prominent band of stagshorn *Acropora*, 1–1·75 m thick, occurs sandwiched between lower and upper layers of sandy calcarenite (0·5–0·75 m and 2–2·5 m thick, respectively). The former contains patches of coral rubble and isolated, *in situ* coral colonies, but the latter is barren. The stagshorn *Acropora* band has a sandy matrix, a well-defined base, and a remarkably level upper surface. It is thought that it developed as a thick bank of branching coral on a gently sloping sands substrate. Indeed, it is likely that the Pleistocene reef in this area developed directly on the lower sands formation, for the latter is well exposed a short distance inland in the Nyali Quarry. Traced inland, the stagshorn *Acropora* passes successively into branching rubble and then back-reef patch facies (Crame 1977, fig. 56). The three quadrats studied at this site (16A–C, text-fig. 1) are separated by horizontal distances of 12 and 20 m, respectively. Their bases were placed at the top of the lower sandy calcarenite and they record reef development at equivalent levels.

Strictly speaking, these quadrats should of course have been included under the heading of succession on shallow-water, unconsolidated substrates, but the assemblages here are so different from all other *Acropora* assemblages studied, and the vertical trends so striking, that they are deemed worthy of consideration within a separate category.



TEXT-FIG. 15. Part of the quadrat studied at Site 16A. *Key*: 1. lower sandy layer, 2. early faviids, 3. early colonies of stagshorn *Acropora* (*Acropora* sp. gp. 4), 4. later colonies of stagshorn *Acropora*, 5. branching *Porites* (*Porites* sp. gp. 1). Horizontal and vertical grid interval: 0.5 m.

Succession at Site 16A (text-figs. 15 and 17) (10 × 1·5 m)

The visual impression of progressive domination by stagshorn *Acropora* (text-fig. 15), is amply confirmed by the analysis (text-fig. 17). In the initial half-metre interval, where coral growth is rather patchy and irregular, small stagshorn colonies are established on the sandy substrate, but so too are corymbose *Acropora* colonies (*Acropora* sp. gp. 3), branching poritids (chiefly *Porites* sp. gp. 1), doming-massive faviids, and several small colonies of *Galaxea fasicularis*. All these forms, however, with the exceptions of *Acropora* sp. gp. 3 and *Porites* sp. gp. 1, become insignificant in the second interval, which is predominantly occupied by stagshorn colonies (text-fig. 17). The latter have increased in both number and size, and clearly, by a process of lateral extension across the substrate, have monopolized nearly all the available habitat space. Domination by stagshorn *Acropora* is virtually complete by the third interval (text-figs. 15 and 17).

Although they do occur at depth on some reef fronts, stagshorn species of *Acropora* are more typical of shallow, sheltered environments on reef flats and in lagoons (e.g. Wells 1954; Davies *et al.* 1971; Stoddart 1973; Pichon 1974). Stagshorn species grow quickly (Vaughan and Wells 1943; Goreau 1961), and once established rapidly cover all available ground space (Braithwaite 1971; Maragos 1974*b*; Connell 1978).

It can be concluded that the reef at Site 16A developed on a flat to gently sloping bank in shallow, open waters. In all probability conditions were similar to those described by Braithwaite (1971) for a reef on the north-east side of Cerf Island (Seychelles), where a prolific stagshorn growth was recorded on a broad, gently sloping bank in depths of no more than 1–2 m.

Succession at Site 16B (text-figs. 16 and 17) (2 × 1·5 m)

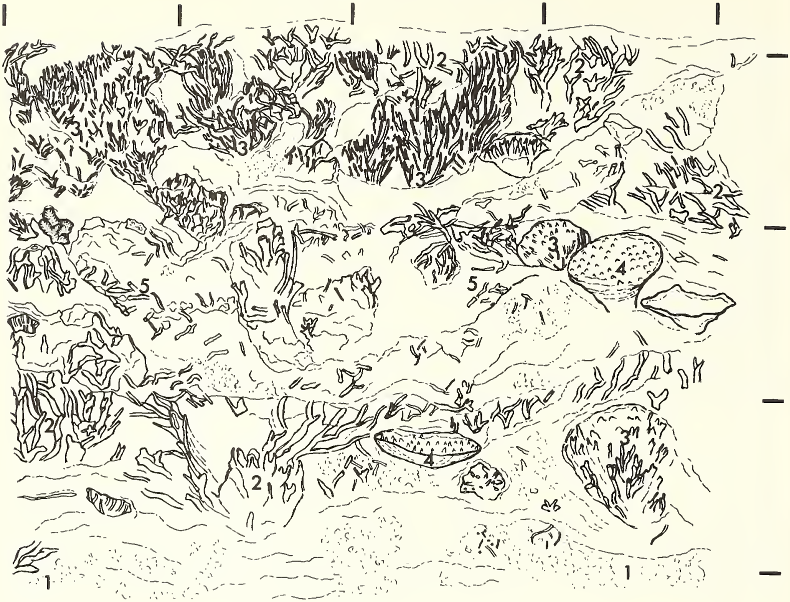
The first interval of this quadrat is dominated by stagshorn *Acropora*, which has clearly established itself on, and grown across, the sandy substrate (text-fig. 16). Other corals that grew directly on the sandy basal layer include *Galaxea fasicularis*, *Acropora hyacinthus* (digitate form—see Appendix), and *Porites* sp. gp. 1. In the second interval the stagshorn maintains its over-all importance (text-figs. 16 and 17), but it has not been able to dominate to the extent that it did at the equivalent level at Site 16A. A range of other coral types (all branching in form) are still found in this interval; these include, *Porites* sp. gp. 1, *A. humilis* (included in *Acropora* sp. gp. 1), and *A. palifera* gp. 4. There is a marked change, however, from the second to the third interval, with the mixed branching assemblage of the former being replaced in the latter by an assemblage dominated by just two coral types, stagshorn *Acropora* and *Porites* sp. gp. 1.

When the trends of individual coral types are plotted out (text-fig. 17), it becomes apparent that branching *Porites* (*Porites* sp. gp. 1) has gradually increased in importance as the reef structure grew, principally at the expense of stagshorn *Acropora*. Small digitate species of *Acropora*, at least in terms of numbers of colonies present, remained relatively constant (text-fig. 17).

Succession at Site 16C (text-fig. 17) (2·5 × 1·5 m)

Coral growth in the initial interval of this quadrat is totally dominated by stagshorn *Acropora* (text-fig. 17). At least three colonies have grown directly off the underlying sands and, by the base of the second interval, a thick mesh of branching coral has been formed. Half-way up the second interval, however, a number of other coral types suddenly appear. These include corymbose *Acropora* (*Acropora* sp. gp. 3), *Pocillopora* sp., and branching *Porites* (*Porites* sp. gp. 1), each of which rests on, and is in turn covered by, stagshorn *Acropora*. As in the quadrat at Site 16B, the mixed coral assemblage of the second interval is replaced by one in the third interval in which only two coral elements (in this instance stagshorn *Acropora* and corymbose *Acropora*) are prominent.

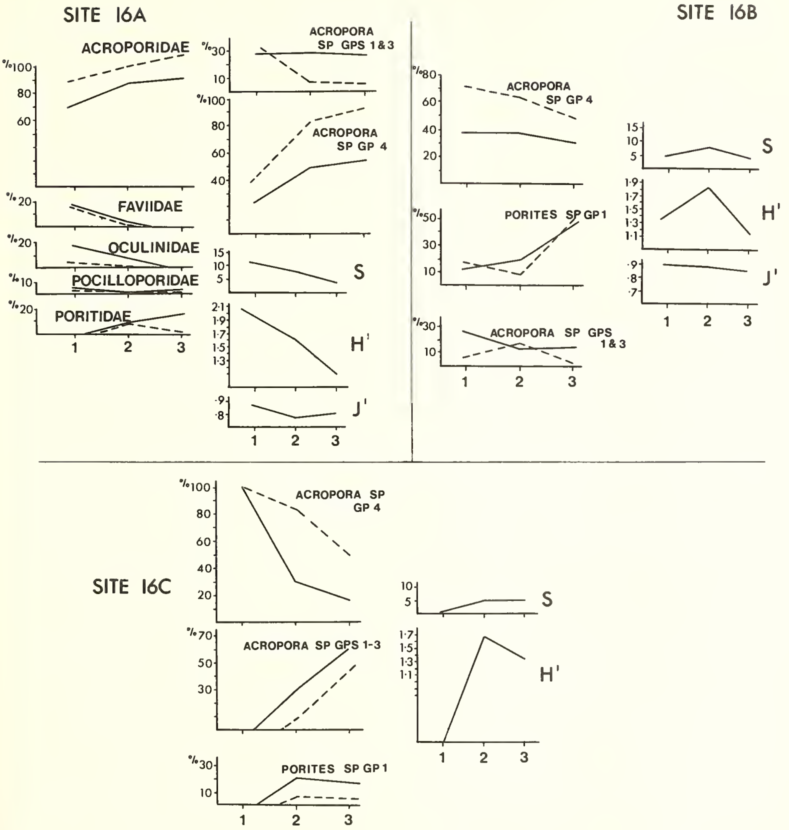
The graphs of the trends for individual coral types (text-fig. 17) clearly show how the corymbose species of *Acropora* (*Acropora* sp. gps. 1–3) gradually increased in importance as the reef structure grew, whereas the stagshorns gradually decreased. It seems that, just as *Porites* sp. gp. 1 displaced stagshorn *Acropora* through the quadrat at Site 16B, so corymbose *Acropora* species displaced it at this site.



TEXT-FIG. 16. The quadrat studied at Site 16B. *Key*: 1. lower branching layer, 2. stagshorn *Acropora*, 3. branching *Porites*, 4. *A. humilis* (*Acropora* sp. gp. 1), 5. loose, rubbly material. Horizontal and vertical grid interval: 0·5 m.

Diversity trends through succession at Sites 16A, 16B, and 16C

The diversity trend for the quadrat at Site 16A reflects the progressive domination of the site by stagshorn *Acropora*. There is a moderately high H' value for the initial coral assemblage, but this falls steeply in the subsequent intervals as the stagshorn becomes increasingly abundant (text-fig. 17). At the other two sites there are low initial H' values due to the early dominance by stagshorn, but higher values in the second interval, where mixed branching assemblages occur (text-fig. 17). In the third interval, however, in both instances, diversity drops again as dominance is re-exerted. The reason for the relaxation in dominance in the middle interval at these two sites is not known for certain, but it may be that an environmental disturbance, such as an abrupt shallowing or storm damage, disrupted the early stagshorn assemblage and allowed other branching types to colonize the area. This may well be one instance of an extrinsic disturbance actually promoting an increase in species diversity.



TEXT-FIG. 17. Coral trends and diversity trends for Sites 16A, 16B, and 16C. The coral trends are given as percentages of the total coral fauna occupied by the principal Families and coral groups at successive half-metre intervals. They are documented in terms of both numbers of specimens (solid line) and Importance Values (dashed line). Diversity trends are given in terms of numbers of species (*S*), the Shannon–Weaver information index (*H′*) and Pielou's measure of equitability (*J′*). The figures on the horizontal axes represent successive half-metre intervals above the base of the quadrat. N.B. Because of the exceptionally low diversity values in the first two intervals, *J′* values have not been calculated for Site 16C.

DISCUSSION

The various successional trends described in this study have been summarized in Table 1. For each of the four categories of reef environment, three stages of development are shown. It should be emphasized that these stages have been selected on a somewhat arbitrary basis to aid comparison of the various successional mechanisms. No hard and fast boundaries exist between them.

Community-control (or obligatory) succession

In view of some of the arguments presented in the introduction, it is perhaps surprising to find a number of instances of community-control succession in the Kenya Pleistocene reef (see categories 1, 3, and 4i, Table 1). This type of succession falls within Connell and Slatyer's (1977) facilitation model and is equivalent to Horn's (1976) obligatory succession model. At Sites 3A, 3B, 3C, and 28,

TABLE 1. Successional trends in the Kenya Pleistocene reef

1. SHALLOW-WATER, UNCONSOLIDATED SANDS		
i. Early domes and mounds formed by clumps of sediment-tolerant corals such as *Galaxea fasicularis* and *Pocillopora*, and doming-massive types such as *Porites* sp. gp. 2, *Favia* sp. gp. 1, *Platygyra*, and *Goniastrea*.	ii. The early mounds extend up into relatively calmer, clearer water and are colonized by the faster-growing branching and platy-encrusting corals (mostly species of *Acropora*).	iii. A thick framework is formed, composed of branching and platy-encrusting types, but with few doming-massive corals.
2. SHALLOW-WATER, FIRM SAND SUBSTRATE		
i. Bare sand is colonized by a mixed assemblage of stagshorn *Acropora* colonies and types such as *Goniastrea retiformis* and *Galaxea fasicularis*.	ii. Stagshorn *Acropora* increases dramatically in both size and numbers of colonies; nearly all other coral types are excluded.	iii. A thick framework of stagshorn *Acropora* is formed which is broken only in places by small stands of coral types such as corymbose *Acropora* and branching *Porites*.
3. SHALLOW-WATER, HARD SUBSTRATE		
i. Doming-massive corals such as *Porites* sp. gp. 2, several faviids, and *Gyrosmilia* colonize the substrate and are subsequently covered by layers of sediment and encrusting corals.	ii. Early mounds extend up into relatively calmer, clearer water and are colonized by branching and encrusting corals (principally species of *Acropora*).	iii. A thick framework of coral is formed, with species of *Acropora* being especially prominent.
4. DEEPER-WATER, SOFT SUBSTRATES		
i. Colonization of the bare (sand) substrate by doming-massive corals (e.g. *Porites*, *Favia*, and *Platygyra*), some of which are subsequently covered by thick layers of encrusting algae.	ii. Colonization of the early mounds by platy and platy-encrusting corals (especially *Montipora* and *Pachyseris*).	iii. Domination of the mounds by thick stands of platy corals (especially *Pachyseris* and *Montipora*).
i. Slow colonization by a small number of platy and thick-branching *Acropora* species (in a *Halimeda*-dominated environment).	ii. Incremental build-up of further *Acropora* species.	iii. Eventual formation of a rich *Acropora* assemblage in which large platy and thick-encrusting species are especially prominent; a few small stands of other branching and encrusting types are also present.

early mounds were formed from a combination of sediment-tolerant and massive coral types such as *Galaxea fasicularis*, *Pocillopora*, *Porites* sp. gp. 2, *Favia* sp. gp. 1, *Platygyra*, and *Goniastrea*. It is assumed that as soon as the tops of these mounds penetrated relatively calmer, clearer water, they were rapidly colonized by faster-growing types, and in particular by branching and platy-encrusting acroporids. These early colonizing corals have all been recorded in similar pioneer roles in recent reef environments. *Pocillopora* is a prodigious early colonizer in Panamá (Glynn *et al.* 1972), Hawaii (Grigg and Maragos 1974; Stimson 1974), and the Red Sea (Loya 1976*a*, *b*), and *Galaxea fasicularis* frequently occurs in isolated stands in shallow, sandy areas (e.g. Rosen 1972). Many species of massive faviid and *Porites* have also been observed as pioneers on sandy bottoms throughout the Indo-Pacific province (Manton 1935; Umbgrove 1947; Wells 1954; Maxwell 1968; Wijsman-Best 1972; Maragos 1974*a*; Mergner and Scheer 1974).

Similar patterns of obligatory succession were observed at Sites 8A and 8B. Here, in what was again thought to have been a shallow-water environment, early doming-massive corals gave the local reef structure a firm foundation and elevated it sufficiently above the rubbly sea floor to allow more sensitive corals (especially species of *Acropora*) to become established in strength. Massive corals are also replaced by branching coral types at Site 5. A number of large *Porites* colonies occur low down in the quadrat at this site, but these are replaced at successively higher levels by numerous small, branching colonies (especially corymbose *Acropora*).

A consistent picture emerges, then, of obligatory succession in shallow-water environments being characterized by an early assemblage of sediment-tolerant corals (some or all of which are doming-massive in form) which is subsequently replaced by an assemblage that is typically rich in branching and platy-encrusting acroporids (i.e. categories 1 and 3, Table 1). Both Mayor (1918) and Manton (1935) recorded living branching *Acropora* species extending across massive faviids, and Talbot (1965, p. 446) suggested that certain shallow-water species of *Acropora* were actually smothering massive *Porites* colonies on Tutia Reef (Tanzania). In a more general way, a number of other authors have indicated that reef development is typified by an initial phase in which massive corals predominate, followed by a subsequent phase of branching and platy-encrusting species (e.g. Umbgrove 1947; Goreau 1959; Mesolella *et al.* 1970; Frost and Langenheim 1974). Braithwaite *et al.* (1973) have shown that the Pleistocene Aldabra Limestone is characterized by a preponderance of doming-massive forms at its base but branching forms at higher levels.

Obligatory succession also occurred in the deeper-water environments of Sites 14A and 14B. In both instances, early assemblages of doming-massive corals cored mounds that were subsequently covered by thick layers of sediment and colonized by platy-encrusting coral types such as *Pachyseris* and *Montipora*. This situation is analogous to that seen on many recent reef fronts (especially at depths in excess of 10 m) where large sheets of platy-encrusting coral frequently grow over a massive foundation (e.g. Goreau 1959).

Although obligatory succession is obviously an important mechanism of reef development, it must be pointed out that it is essentially restricted to the earliest stages of reef development on a bare substrate. It is hard to find evidence of obligatory sequences at higher levels and it is likely that, once a framework has been established, further succession is governed principally by the more cryptic influences of interspecific competition and extrinsic disturbances.

Random, non-directional trends

Apart from the early obligatory sequences, there is little evidence of clear-cut directional trends in the sections studied. Only very generalized stages of reef development can be recognized (Table 1), and among the principal frame-building species there appear to be no more than two broad categories of colonizing strategy (early and later colonizers, Table 2). Even the community-control (or obligatory) sequences are far from constant in terms of species composition, for we have seen how there is a variety of pioneers on both soft and hard substrates, and many different species that can subsequently replace them. Quite why succession should appear to be so unstructured and haphazard is at first perplexing, but a plausible explanation can perhaps be found by recourse to theoretical arguments put forward in the introduction.

TABLE 2. Ecological roles of the principal frame-building corals in the Kenya Pleistocene reef

	3A	3B	3C	28	6	14A	14B	8A	8B	5	16A	16B	16C
Pocillopora sp. gp. 1			E										
sp. gp. 2			E										
sp.	L	L	E	L				L			E		
Acropora sp. gp. 1													
sp. gp. 2				L	L								
sp. gp. 3	L	L	L	L	L			L	L	L	E–L		L
sp. gp. 4											E–L	E–L	E–L
sp. gp. 6									L				
sp. gp. 7	L	L	L	L	L			L	L	L			
sp. gp. 8					L				L				
palifera gp. 1			L		E–L			L					
gp. 2			L	L				L		L			
gp. 3			L		L								
gp. 4												L	
Astreopora horizontalis de Blainville				L				L					
Montipora sp.				L		E–L	L						
Pavona clavus (Dana)			L										
Pavona sp.			L										
Pachyseris sp.						L	L						
Porites sp. gp. 1										L	L	L	L
sp. gp. 2			E	E–L	E	E	E–L	E	E				
Alveopora sp.									L				
Favia stelligera (Dana)	E	E		L									
Favia sp. gp. 1		E		E		E		E					
Goniastrea retiformis (Lamarck)	E							E			E		
Goniastrea pectinata (Ehrenberg)							L						
Goniastrea sp.				L									
Platygyra lamellina (Ehrenberg)	E			E									
Platygyra sp.	E	E		E		E							
Leptoria phrygia (Ellis and Solander)				E–L									
Hydnophora microconos (Lamarck)				L									
Diploastrea heliopora (Lamarck)				L									
Leptastrea sp. gp. 2				L									
Echinopora sp.	L	L											
Galaxea fasicularis (Lamarck)	E	E		E						L	E		
Acanthastrea echinata (Dana)				L									
Lobophyllia corymbosa (Forskål)				E									
Gyrosmilia sp.									E				

Key: E—early colonizer; L—later colonizer; E–L—both early and later colonizer.

In Connell and Slatyer's (1977) inhibition model there is no ecological succession until an extrinsic disturbance damages or destroys one or a small number of established residents: any available species may then colonize the newly created opening. Thus, extrinsic influences such as storm damage, predation, or the effect of pathogens will govern the course of ecological succession. Such influences are known to be widespread on coral reefs (Grassle 1973; Connell 1976, 1978; Loya 1976*c*) and it is likely that they will occur on a time scale shorter than that required for intrinsic community development (Drury and Nisbet 1973, p. 358). Golley (1977, p. 329) has summarized the situation succinctly when he states, '. . . the response of the community to disturbance through succession is more significant than the possible orderly sequence of communities in space or time. The essence of succession may well be response not pattern.'

In a recent review of species diversity in tropical rain forests and coral reefs, Connell (1978) has argued that corals (and trees) are very generalized in their resource requirements. He could find no evidence to suggest that corals had partitioned either their habitats or trophic resources to the extent that would be necessary to bring about the very high observed diversities. Coral reefs (and rain forests) are not the highly integrated, co-evolved species complexes that they have traditionally been assumed to be. Disruptions (physical disturbances, predation, etc.) are probably so frequent that equilibrium conditions are rarely attained. The continually fluctuating conditions prevent any one species or group of species from monopolizing resources and thus maintain a high species diversity. They also actively promote the continual formation of clearings in reefs and forests that permits the widespread occurrence of inhibition succession. Random sequences can thus be expected, *a priori*, to be the rule rather than the exception on established coral reefs.

Competition in early succession

It is unlikely, however, that all ecological successions will be entirely random, non-directional processes governed only by the nature and extent of extrinsic disturbances. The inhibition model of succession relates primarily to secondary successions on well-established reefs. At earlier stages of reef development interspecific competition must surely occur, for there will almost certainly be a distinct phase of replacement of early colonizers by later arrivals.

There is as yet insufficient data on the life histories, dispersal powers, and competitive abilities of most hermatypic corals to enable them to be classified as either **r** or **K** strategists. Pocilloporids, however, are one group that consistently show **r** strategist characters (Loya 1976*a*, *b*), and at Site 3C *Pocillopora* is certainly a prominent early colonizer. Doming-massive faviids and *Porites* are also important pioneers (Table 2), but their large size and comparatively slow growth rates preclude them from being considered as **r** strategists in the strict sense. However, it is interesting to note that on reef flats in the Gulf of Eilat (Red Sea), small encrusting faviids and *Porites* adopt opportunistic roles (Loya 1976*c*). *Galaxea fasicularis*, a prodigious early colonizer, occurs as numerous small, spiky colonies and is widely dispersed throughout the Kenya Pleistocene reef. It is here provisionally classified as an **r** strategist along with the pocilloporids.

We have already discussed how pioneer coral assemblages tend to be rapidly colonized and dominated by faster-growing branching and platy-encrusting corals. At Site 5, for example, an early *Porites*-dominated assemblage is replaced by a thick corymbose *Acropora* assemblage, and at Sites 8A and 8B early mounds, based on doming-massive corals, were rapidly colonized by a mixture of branching and platy-encrusting *Acropora*. At Site 16, stagshorn *Acropora* was seen to be an extremely effective competitor, rapidly outgrowing other early colonizers to form large, monospecific stands. Clearly, in any competitive hierarchy between shallow-water reef species, branching and platy-encrusting species (and especially acroporids) are likely to predominate. Instances have been recorded of massive corals resisting overgrowth (e.g. Connell 1976, p. 52), but as a general rule we can assume that the slower-growing massive corals will rank lower in competitive ability to most branching and platy-encrusting types (cf. Connell 1976, table 1). Besides stagshorn *Acropora* (*Acropora* sp. gp. 4), other species likely to rank high in competitive hierarchies within the Kenya Pleistocene reef are *Acropora* sp. gps. 3 and 7, *A. palifera* gp. 2, and *Porites* sp. gp. 1 (Table 2). It may be concluded, therefore, that the principal short-term successional trend on many shallow-water reefs (i.e. those in approximately the 2–10 m depth range) will be rapid domination by branching and platy-encrusting corals, and in particular by acroporids.

In deeper-water environments, such as at Sites 14A and 14B, branching and platy-encrusting corals will in some cases be competitively subordinate to certain coral types with large platy and sheet-like colonies (such as *Pachyseris* and *Montipora*). Although not necessarily faster-growing, such colonies are more efficient at occupying space in the light and thus absorbing more of the incident light energy.

Longer-term trends

We may also expect to find some pattern to the later phases of reef development. Inhibition succession is characterized by a gradual introduction of longer-lived species and thus we might expect to see the gradual domination of a reef by large, massive corals: Grime (1977, p. 1189) has shown that a consistent feature of vegetation succession is the incursion of plants of greater size. In broad terms, we should expect a progressive replacement of small colonies (of all types) by large, massive ones. The former will be initially more successful in securing space, but in time they will be replaced by more durable, massive forms. It should be emphasized that this is a much slower, longer-term process than any of the other successional replacements outlined above. In both coral reefs and tropical forests, the gradual rise to dominance of assemblages of large species probably involves time-spans of several hundreds of years.

Some evidence of a trend towards eventual domination by large, massive colonies comes from Sites 6 and 28. At Site 6, massive encrusting colonies of *A. palifera* become increasingly important at higher levels (text-fig. 8), and at Site 28 the reef mound is capped by several large, doming-encrusting faviids (text-fig. 7). The large size and gradual rise to dominance of corals such as these are features suggestive of **K** strategies.

Long-term domination by slower-growing doming-massive corals can also be predicted by considering a relationship between temporal sequences of species and spatial sequences along stress gradients. Drury and Nisbet (1973, p. 358) have pointed out that species prominent in the early stages of succession (opportunists or **r** selected species) are characteristic of high-stress sites on environmental gradients, whilst those prominent in the later stages (equilibrium or **K** selected species) are characteristic of the low-stress end. Now it is well known that corals occur on recent reefs in distinct zones (see, e.g., the review by Rosen 1975) and that the principal cause of the zonation is response to an environmental stress gradient. Consequently, might not the coral zonation patterns we see on recent reefs reflect a potential temporal zonation? In his scheme for Indo-Pacific reefs, Rosen (1975) has established the following five zones (or associations) on the basis of faunal response to a stress gradient of water movement: (i) Calcareous algae, (ii) *Pocillopora*, (iii) *Acropora*, (iv) Faviids, (v) *Porites*. The zones intergrade from the shallow-water (high-energy) Calcareous algae zone to the deep-water (low-energy) *Porites* zone. If left to develop uninterrupted, an Indo-Pacific reef would therefore be expected to show a temporal sequence of zones grading from Calcareous algae to *Porites*. Thus in time *Pocillopora* assemblages might be replaced by *Acropora*-dominated assemblages and the latter by massive faviid and poritid assemblages. Massive corals can indeed resist overgrowth by faster-growing species (Lang 1971, 1973; Connell 1976), and over an extended period of time it would be possible for them to eventually dominate a reef. However, such long-term transitions have yet to be convincingly demonstrated in either fossil or recent reefs.

Diversity through succession

A long-standing tenet of ecology has been that complex tropical ecosystems are inherently stable. However, powerful theoretical arguments have recently been advanced against this stability–diversity concept (e.g. May 1973) and it is now thought that tropical high diversity is as much the product of a constantly fluctuating environment as it is of extensive resource partitioning in a benign environment (e.g. Connell 1978). If small, localized disturbances are continually occurring on a reef, we can expect no consistent pattern of species diversity change through succession. Clearly, the process of incorporating further species into the reef will be continually interrupted.

In this study four generalized categories of diversity change through succession have been recognized.

i. Diversity increase in a constant environment

At Sites 6 and 28 species diversity continues to increase through succession (H' values, text-figs. 6 and 9). In both instances there is an abrupt early rise in diversity followed by smaller increases at higher levels. The sharp increase in the species richness component (S) at both sites in the early stages most likely represents an initial phase of species immigration, whilst the increase in J' values in the highest intervals (text-figs. 6 and 9) reflects an increase in species evenness. An early rise in species richness followed by an increase in species evenness is probably the mechanism by which coral species diversity is continually built up in any constant reef environment.

ii. Diversity decrease in a constant environment

At Site 16A diversity falls continually through succession (H' values, text-fig. 17) as the original mixed assemblage is progressively dominated by stagshorn *Acropora*. There is no evidence of a break in the faunal sequence at this site and thus it would appear to be a genuine instance of succession being accompanied by a reduction in species diversity. Similar reductions in diversity caused by dense overgrowths of branching *Acropora* have been recorded on several recent reefs (e.g. Connell 1978, pp. 1304–1305; Talbot 1965, p. 447).

iii. Diversity increase in a fluctuating environment

At Sites 16B and 16C diversity rises sharply from the first to the second interval (H' values, text-fig. 17) when early dense stands of stagshorn *Acropora* are replaced by mixed coral assemblages. It is thought likely that localized extrinsic disturbances (such as damage by predators or a storm, or the effects of a low spring tide) created openings in the stagshorn stands at these sites that subsequently allowed other coral types to become established. Thus it is possible, under certain circumstances, for a fluctuating environment to actually promote an increase in species diversity.

iv. Diversity decrease in a fluctuating environment

The abrupt falls in the diversity trends for Sites 3A, 3B, 3C, 5, 8A, and 8B (H' values, text-figs. 6 and 14) would seem to be due to the effects of localized dominance. Small clearings are continually created on reefs (as outlined above) and in theory these can then be colonized by any available species. However, on most shallow-water reefs such clearings will be rapidly colonized by certain coral types such as the faster-growing ones, or those with more efficient means of dispersal. One or a small number of such types will rapidly pre-empt the greater part of the available habitat space and effectively preclude other corals: as a direct consequence diversity drops sharply. *Acropora* species acted as dominants at Sites 3C, 5, 8A, and 8B, *Galaxea fasicularis* at Site 3B and doming-massive faviids at Site 3A.

No attempt has yet been made to study longer-term diversity trends in the reef. Theoretical arguments predict a steady increase in diversity through succession, followed by a levelling-off when the equilibrium number of species (or climax assemblage) for a particular area is reached (e.g. Odum 1969; Simberloff and Wilson 1969; Grigg and Maragos 1974; Osman and Whitlach 1978). By increasing the size of quadrats and incorporating data from recent assemblages, it may be possible to document the point at which such asymptotic levelling occurs for various reef environments. Data from sites such as 6 and 28 (text-figs. 6 and 9) suggest that equilibria may perhaps be attained within as little as 2 m of vertical development. At both these sites, the 'equilibrium' number of species in the assemblage would appear to be approximately 20 (text-figs. 6 and 9).

Other factors influencing succession

It was stated in the introduction that the main reef limestones of the Kenya coast are believed to be the product of a single depositional event during the last Interglacial. Although conditions are thought to have been relatively constant during this event, it is likely that minor fluctuations in water depth (and thus in parameters such as the intensity of water movement) constantly occurred. Consequently, it could be argued that some of the trends described in this study reflect no more than a gradual change in coral faunas in response to an environmental gradient (such as increasing water depth). This is particularly so at sites where early constructional domes are replaced by a later mixed-coral framework. Might not these early domes indicate reef development in a comparatively shallow, high-energy environment, and the later framework development in a progressively deeper, quieter-water environment? This could indeed be the case, but it is here maintained that extrinsic factors can at best only be partially responsible for any of the observed faunal trends. All environments tend to fluctuate, and all but the swiftest successions must take place in a relatively inconstant environment. In practice it has proved extremely difficult to separate the roles of intrinsic and extrinsic factors in ecological successions and thus to assess their relative importance (Kershaw 1973, p. 42; Odum 1971, p. 255; Walker and Alberstadt 1975, p. 238). Taking into account both sedimentary and faunal evidence, it seems unlikely that extrinsic factors exerted any undue influence on any of the trends described here.

Obviously other organisms must play an important part in determining the course of reef succession, but their effects are usually hard to assess in the fossil record. Other sessile organisms (soft corals, algae, sponges, etc.) will compete with corals for the occupancy of available habitat space and patterns of coral distribution and colonization could be seriously disrupted by the activity of predators.

The demonstration of interspecific aggression between scleractinian corals (Lang 1971, 1973; Connell 1973, 1976) has important implications for successional studies as it has been shown that on certain reefs corals can be arranged into natural aggressive hierarchies or 'pecking orders'. However, little work has yet been carried out on the aggressive hierarchies of Indo-Pacific corals.

CONCLUSIONS

In studies of fossil reef succession, geologists should concentrate less on establishing successive zones or stages and more on examining the roles of individual species. Theories based on community-control, i.e. the notion that one set of species in some way 'prepares the ground' for the next, have now been largely superseded by theories based on the interactions of individuals with each other and with the physical environment.

Community-control (or obligatory) succession can, however, be observed in the earliest stages of reef development on a bare substrate. Pioneer assemblages of tolerant and robust corals form low but distinct mounds that are subsequently colonized by assemblages dominated by more sensitive species. Prominent among the latter are many faster-growing branching and platy-encrusting types.

The lack of clear-cut stages (or zones) in the sections studied reflects the random nature of reef succession. Theories based on extrinsic as opposed to intrinsic community-controls predict that any available species can colonize an opening on an established reef and, in time, random, unstructured faunal sequences may be built up.

However, there is some pattern to the early stages of reef succession, as early colonizers are replaced by later arrivals. Competitive interactions occur between individuals and there is evidence that many pioneer species are replaced by faster-growing branching and platy-encrusting types. The principal short-term successional trend in many shallow-water reefs (i.e. those in approximately the 2–10 m depth range) appears to be fairly rapid domination by *Acropora* assemblages.

Longer-term trends are harder to discern but there is some evidence to suggest that, if left undisturbed, many reefs will eventually be dominated by large doming-massive and encrusting colonies. In time, *Acropora*-dominated assemblages could be replaced by massive faviid and poritid assemblages.

There are no consistent short-term diversity trends in the Kenya Pleistocene reef. Adjacent sites show contrasting trends and there is evidence that patterns of species diversity are strongly controlled by localized environmental conditions. Longer-term trends have yet to be fully investigated, but it is possible that in some areas equilibrium assemblages were established within 2 m of vertical development.

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APPENDIX

NOTES ON CORAL NOMENCLATURE AND SPECIES GROUPING

Pocillopora sp. gp. 1: the more delicate branching forms of *Pocillopora*; generally small colonies; this group embraces both delicate forms such as *P. damicornis* (Linnaeus) and more robust species such as *P. danae* Verrill and *P. meandrina* Dana (cf. Rosen 1971, p. 169).

Pocillopora sp. gp. 2: forms with stouter, longer branches; generally larger colonies; typified by *P. eydouxi* Milne-Edwards and Haime.

Acropora sp. gp. 1: the *A. humilis* (Dana) group, following the interpretation of *A. humilis* by Wells (1954, p. 425).

Acropora sp. gp. 2: the *A. hyacinthus* (Dana) group, based on the descriptions of the species *M.* (*Madrepora*, later *Acropora*) *cytherea* Dana, *M. armata* Brook, *M. hyacinthus*, and *M. reticulata* Brook by Brook (1893); see also the grouping of *A. hyacinthus*, *A. cytherea*, and *A. reticulata* by Wells (1954, p. 422). Somewhat less satisfactorily, forms resembling *A. irregularis* (Brook) have also been included in this group. A short working definition of the group is as follows: small colonies with short, thin, pointed branches; each branch giving rise to several side branches; colony shape either corymbose or horizontally branching.

Very large colonies of *A. hyacinthus* also occur; in particular, large, thick-sheet form colonies occur in shallow, protected sites on a number of reefs (e.g. Talbot 1965; Braithwaite *et al.* 1973).

Acropora sp. gp. 3: *Acropora* of the types covered by groups 1 and 2 but not well enough preserved to be confidently assigned to either of these groups.

Acropora sp. gp. 4: stagshorn *Acropora*; principally *A. formosa* (Dana) (Wells 1954, p. 415; see also Rosen 1971, p. 172).

Acropora sp. gp. 6: the *A. conferta* group (see Brook 1893, p. 108); colony bases formed of a mesh of horizontal branches; short, spiky upright branches rise up from the base.

Acropora sp. gp. 7: platy-encrusting *Acropora* that cannot be readily grouped with other platy-encrusting types (i.e. the platy-encrusting forms of *A. hyacinthus* or *A. palifera*); plate thickness generally less than 3 cm.

Acropora sp. gp. 8: thick-encrusting and massive *Acropora* that cannot be definitely assigned to the *A. palifera* (Lamarck) group.

A. palifera: included in this group is *A. cuneata* (Dana), a form which closely resembles *A. palifera* (Wells 1954, pp. 429–431). Brook's descriptions of the species comprising his subgenus *Isopora* (*M. palifera*, *M. palifera* var. α, *M. hispida* Brook, *M. securis* Dana, *M. cuneata* Dana, and *M. plicata* Brook) were also used in the determination of this group (Brook 1893, p. 131).

A. palifera gp. 1: embracing both *A. palifera* forma α and *A. palifera* forma β of Wells (1954); the thick-branching types.

A. palifera gp. 2: a rather unusual group that has distinctly platy colonies; generally no more than 3 cm thick; some plates are up to 1 m across; the exact systematic status of this group is uncertain.

A. palifera gp. 3: thick, massive-encrusting types.

A. palifera gp. 4: a form with prominent 'blades' rising from a hummocky base; closely resembling the holotype of *A. securis* (Dana) (Wells 1954, pl. 133) (which is now included in *A. cuneata* (Dana)—Wells 1954, p. 429).

Porites sp. gp. 1: the branching species of *Porites*; principally forms that closely resemble both *P. andrewsi* Vaughan and *P. nigrescens* Dana.

Porites sp. gp. 2: the massive species of *Porites*; principally forms that resemble species such as *P. lutea* Milne-Edwards and Haime and *P. solida* (Forskål).

Favia: accurate identification of the various species within this genus proved to be extremely difficult. Even though numerous descriptions of the principal large-calice forms are available (e.g. Matthai 1914; Vaughan 1918; Wells 1954; Rosen 1968; Wijsman-Best 1972), is was impossible to divide the specimens from the Kenya Pleistocene reef into meaningful species groups. The three commonest large-calice species, *F. favus* (Forskål), *F. speciosa* (Dana), and *F. pallida* (Dana), are here combined as *Favia* sp. gp. 1. *F. stelligera* (Dana), by virtue of both its growth form and calical configuration, is a distinctive species (see, e.g., Vaughan 1918, p. 101).

Leptastrea sp. gp. 2: principally *L. bottae* (Milne-Edwards and Haime) and *L. immersa* Klunzinger; a group with large, prominent, subcircular calices.

THE STRUCTURE, FUNCTION, AND EVOLUTION OF TUBE FEET AND AMBULACRAL PORES IN IRREGULAR ECHINOIDS

by ANDREW B. SMITH

ABSTRACT. The variation in the tube foot morphology of twenty species of Recent irregular echinoids, with representatives from all four principle groups, is described and correlated with the structure of the associated ambulacral pores. Tube feet are often highly modified and sensory, respiratory, suckered, feeding, and funnel-building tube feet are all described. Three types of pore are recognized—isopores, anisopores, and unipores—and these are further subdivided on the basis of pore size and shape, size and position of the neural canal, development of an attachment area, and the extent of the periporal area.

Tube foot morphology is interpreted in functional terms and related to the animal's mode of life. Functionally significant features of pores include their shape and size, the number of pores, their divergence, and the attachment and periporal areas. The structure and arrangement of pores can often be used to identify the morphology and function of the associated tube foot.

The evolution and diversification of irregular echinoids is seen as a direct consequence of changes in feeding method. Primitive irregulars had abandoned grazing or scavenging for selective particle ingestion and rapidly diversified as bulk sediment swallowers in less organic-rich substrates. Like Recent holectypoids and cassiduloids, the early groups appear to have used suckered tube feet for feeding and were thus restricted to coarse sediments. By the Cretaceous, mucous adhesive tube feet had developed in the disasteroids enabling them to feed on finer substrates and spatangoids and holasteroids probably evolved from an ancestor with penicillate tube feet. Clypeasteroids evolved from cassiduloids initially to gain access to finer sediments. Pourtalesiids have evolved a feeding mechanism that does not involve tube feet.

TUBE feet are undoubtedly organs of great importance to the echinoderms. These external extensions of the water vascular system are found in all extant classes of the phylum Echinodermata, but the variation in tube foot structure and function that occurs in irregular echinoids surpasses that found in any other group of echinoderms. In irregular echinoids the adoption of a buried mode of life has been accompanied by a marked specialization and diversification of the tube feet. As well as sensory and suckered tube feet, which also occur in regular echinoids, irregular echinoids may possess tube feet especially modified for mucus secretion, gaseous exchange, feeding, and funnel-building. Accompanying this diversification in tube foot structure and function there is a corresponding change in the pore, or pores, through which each tube foot connects with its internal ampulla.

Although the morphology of the tube feet of irregular echinoids is relatively well known, from external descriptions and histological studies by such workers as Lovén (1883), Hamann (1887), Nichols (1959*a*, *c*), and Fenner (1973), the corresponding variation in pore morphology has been largely ignored from a functional point of view. Only Lovén (1883) has described and illustrated a variety of tube feet and their associated ambulacral pores, though he made no attempt to correlate pore morphology with tube foot structure, and gave no functional interpretations. Nichols (1959*a*, *b*) has described the tube feet and ambulacral pores in the spatangoid *Echinocardium cordatum* and suggested that pore morphology could be used to help reconstruct the tube feet of fossil echinoids. Analysis of the functional morphology of the coronal pores of regular echinoids (Smith, 1978*b*) has shown that pore morphology and tube foot morphology are closely linked.

[Palaeontology, Vol. 23, Part 1, 1980, pp. 39–83, pls. 1–6.]

With the exception of the elongate pores making up the petals, which are generally known to bear specialized respiratory tube feet, the functional significance of the different pore morphologies is poorly understood. This paper sets out to describe the variation in ambulacral pores of irregular echinoids and to correlate this with the variation in tube foot morphology. Once the functional significance of the pore morphology in Recent species is better understood it should be possible to reconstruct the tube feet of fossil species with more certainty. A knowledge of the probable tube foot morphology in fossil species can be extremely helpful in palaeobiological studies as has been shown by Nichols (1959*b*) and Smith (1978*a*).

MATERIALS AND METHODS

A histological study of the tube feet of a variety of irregular echinoids, listed in Table 1, was carried out using the method outlined in Smith (1978*b*). Each species was examined under a light microscope to identify areas bearing different tube feet and a number of tube feet from each area were sectioned. The pore morphology associated with each type of tube foot was studied by placing cleaned and gold-coated pieces of test under a scanning electron microscope (SEM). Stereo electron micrographs were taken by rotating the stage through 7½ degrees and re-centring. In addition the morphology of the tube feet and pores was examined in a number of other Recent species by means of a binocular microscope. Ambulacral pores of a number of fossil species have also been examined using the SEM.

TABLE 1. Recent species in which the tube feet were examined histologically

HOLECTYPOIDA

Echinoneus cyclostomus Leske

CASSIDULOIDA

Apatopygus recens (Milne-Edwards)
Cassidulus cariboearum Lamarck
Echinolampas crassa (Bell)

CLYPEASTEROIDA

Clypeaster rarispina de Meijere
C. rosaceus (Linnaeus)
Dendraster excentricus (Eschscholtz)
Echinocyamus pusillus (Müller)
Echinodiscus bisperforatus Leske
Mellita quinquiesperforata (Leske)

HOLASTEROIDA

Pourtalesia miranda Agassiz
Urechinus wyvilli (Agassiz)

SPATANGOIDA

Aeropsis rostrata (Wyville Thomson)
Brissopsis lyrifera (Forbes)
Echinocardium cordatum (Pennant)
E. pennatifidum Norman
Hemiaster expurgitus Lovén
Metalia sternalis (Lamarck)
Palaeostoma mirabile (Gray)
Spatangus raschi Lovén

NOMENCLATURE

The area of the test, to which each tube foot attaches, is perforated by a single or double pore, and the plate surface surrounding the pore or pores is typically modified to accommodate the base of the tube foot. Where this area contains two more or less equally sized pores, then it is described as an *isopore*. Where the two pores differ markedly in size it is termed an *anisopore*. Where only a single pore is present then the area is described as a *unipore*. Much of the terminology applied to ambulacral pores has been given in Smith (1978*b*) and it is only necessary to mention briefly a number of those terms that are to be used throughout this paper. The *attachment area* is defined as that area of the plate surface into which the connective tissue fibres of the tube foot insert. The stereom of the attachment area is modified for fibre insertion. Where there are very few connective tissue fibres to accommodate, as in some respiratory tube feet, no stereom modification occurs and the attachment area is said to be absent. If the stereom is not well preserved the attachment area can often be recognized by the fact that it usually forms an elevated rim around the pore or pores. The area which lies within the attachment area and which surrounds the pore or pores is termed the *periporal area*. This is covered in life with squamous epithelium and is best developed in certain unipores. In isopores and anisopores the pore lying nearer to the perradial suture is the *perradial pore*. This pore accommodates a branch of the radial nerve which, when well developed, lies in a groove—the *neural canal*. The other pore, lying nearer the adradial suture, is termed the *adradial pore*. In some cases the two pores may lie in an adoral/adapical orientation so that the perradial pore takes up an adoral position relative to the adradial pore. The area which lies directly in between the two pores is the *interporal partition*.

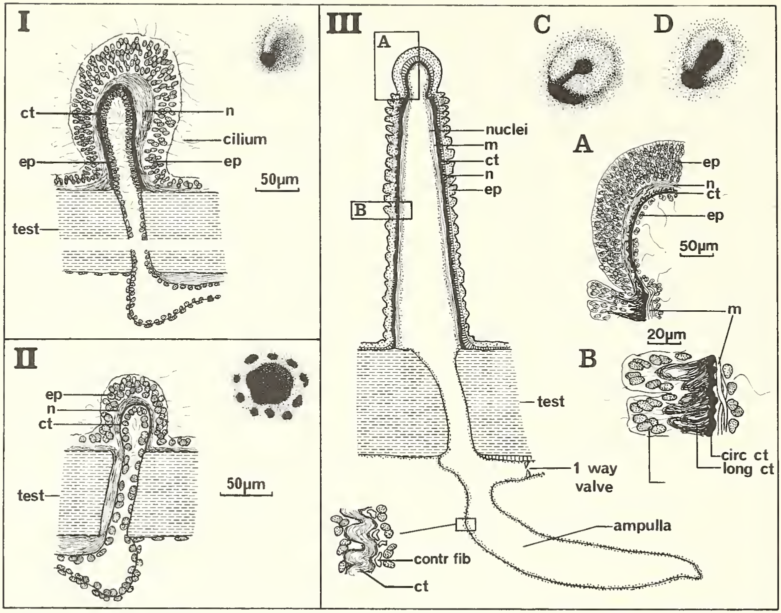
TUBE FOOT MORPHOLOGY

Before discussing the functional morphology of ambulacral pores, it is necessary to outline the morphology of the tube feet of irregular echinoids. These tube feet show considerable morphological variation and can be arranged into the following functional groups.

Sensory tube feet (text-fig. 1). The simplest of tube feet are those found ambitally in the lateral and posterior ambulacra of some spatangoids, as in *Echinocardium cordatum* (text-fig. 1ii). Above each unipore there is a small mound of sensory epithelium. The lumen is small and extends only slightly above the level of the test. A thin connective tissue layer separates the ectodermal cells from the endothelial cells, both of which are densely ciliated. Muscle fibres are absent and there is no ampulla, thus these tube feet are apparently non-extensible. Much of the pore space through the test is taken up with nervous tissue and there is a thick nerve plexus which underlies the epithelial cells of the tube foot. This tube foot is similar in construction to the terminal tube foot of ocular plates. These tube feet are presumably chemo-sensory in function.

A similar type of tube foot is found at the apex of the anterior ambulacrum of *Brissopsis lyrifera* (text-fig. 1i). Here the ten or twelve most adapical tube feet are squat and bulbous and are richly endowed with nerve fibres and cilia. Stem muscle fibres and an ampulla are again absent indicating that these tube feet are also non-extensible. These tube feet, as well as being important chemo-sensory receptors, are also likely to enhance cilia-induced water movement down the anterior ambulacrum.

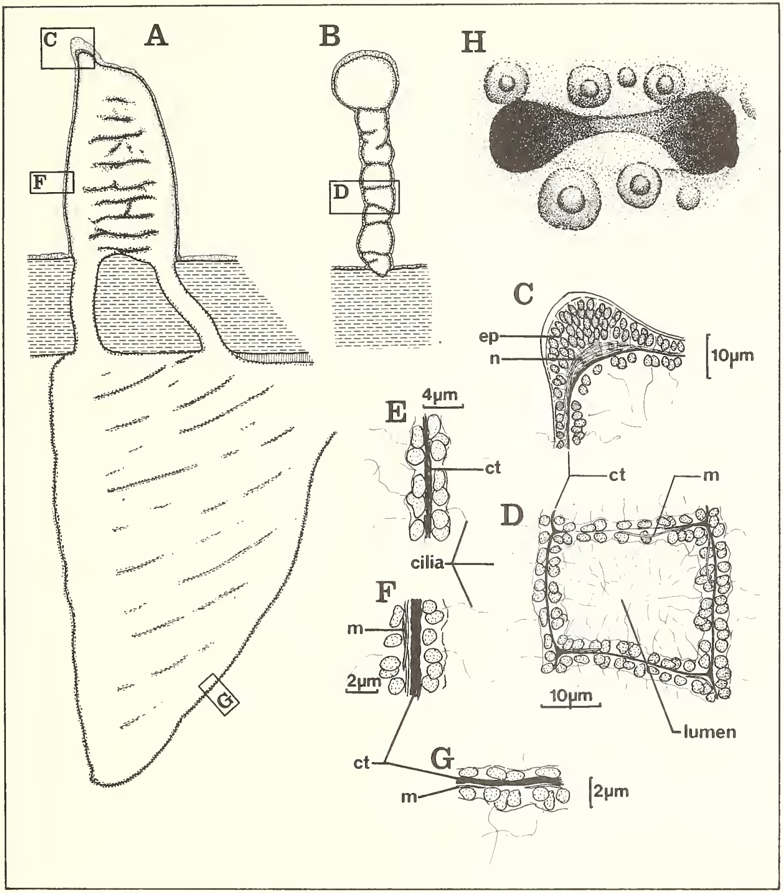
In the majority of spatangoids, the sensory tube feet that occur between the petals and the phyllodes are long and extensible. The stem, which has a few muscle fibres as well as circular and longitudinal connective tissue fibres, terminates in a cap of dense epithelial cells underlain by a thickened nerve plexus (text-fig. 1iii). The connective tissue layer of the tip commonly incorporates spicules or, occasionally, sheet-like elements, composed of a single layer of trabeculae (see Lovén 1883, pl. X). The associated ampulla is small and cylindrical. There are obvious bands of contractile fibres which branch and interconnect with one another as illustrated by Nichols (1959*c*, fig. 5) for the cylindrical ampullae of a clypeasteroid. The lumen of the ampulla is not crossed by septa. These tube feet are extensible and probe the surrounding substrate. In spatangoids, all ambital tube feet in ambulacrum III have this structure. In addition, the aboral tube feet in ambulacrum III of certain species are also sensory. Finally, in the holasteroids *Urechinus naresianus* and *Pourtalesia*



TEXT-FIG. 1. Sensory tube feet. I, longitudinal section through an apical tube foot in ambulacrum III of *Brissopsis lyrifera* and the associated unipore. II, longitudinal section through an ambital ambulacrum IV tube foot of *Echinocardium cordatum* and the associated simple unipore. III, longitudinal section through an ambital ambulacrum I tube foot and ampulla of *Spatangus raschi*: A and B, detailed structure of terminal pad and stem as indicated: C, ambital ambulacrum III unipore of *S. raschi*: D, aboral ambulacrum III unipore of *Pourtalesia miranda*. Abbreviations used in text-figs.: circ ct = circular connective tissue; contr fib = contractile fibre; ct = connective tissue; cyt septum = cytoplasmic septum; ep = epithelium; long ct = longitudinal connective tissue; m = muscle; muc cells = mucus cells; n = nerve.

miranda aboral respiratory tube feet are lacking and in their place are found simple sensory tube feet borne upon unipores. In *Pourtalesia* these are no more than minute, non-extensible sensory mounds but in *Urechinus* they are slightly larger.

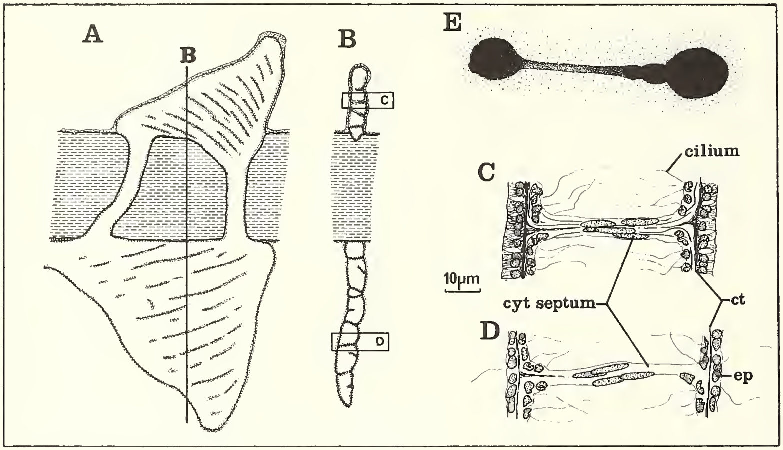
Respiratory tube feet (text-figs. 2–5). Tube feet that are specialized for gaseous exchange are always associated with isopores or anisopores. The lumen of such tube feet is divided into two large tubular channels separated by a thin-walled central area. This central region is crossed by epithelial septa, each with a thin core of connective tissue, which effectively partitions the lumen into narrow, parallel passageways connecting the two major channels (text-fig. 2). In its simplest form this central region is planar with the parallel passageways stacked one above the other (text-figs. 2, 3). This is the case in tube feet of cassiduloids, most clypeasteroids, and a few spatangoids. The tube foot may either be tall and approaching bilateral symmetry (text-fig. 2), as found in the respiratory tube feet of arbacioids (Fenner 1973; Smith 1978*b*), or may be strongly skewed towards the adradial pore



TEXT-FIG. 2. Aboral respiratory tube foot and ampulla of *Apatopygus recens*. A, longitudinal section; B, sagittal section; C, D, F, G, details of structure as indicated; E, longitudinal section through part of the stem of a respiratory tube foot of *Cassidulus cariboearum*; H, aboral conjugate isopore of *A. recens*.

where the tip may be developed into a sensory pad (text-fig. 3). In *Clypeaster rarispina* and *B. lyrifera* lobes extend from the central region of respiratory tube feet increasing the surface area (text-fig. 4). Larger lobes are septate.

The petal tube feet in spatangoids such as *E. cordatum* and *Spatangus raschi* are exceedingly convolute making the reconstruction of the precise three-dimensional appearance of these tube feet extremely difficult. Longitudinal, sagittal, and transverse sections through respiratory tube feet of *Spatangus* are given in text-fig. 4. From these it appears as though the central region of the tube foot gives off prominent branched and lobed outpouchings which are partitioned by septa. In some instances these outpouchings appear to be better developed on one side of the tube foot.

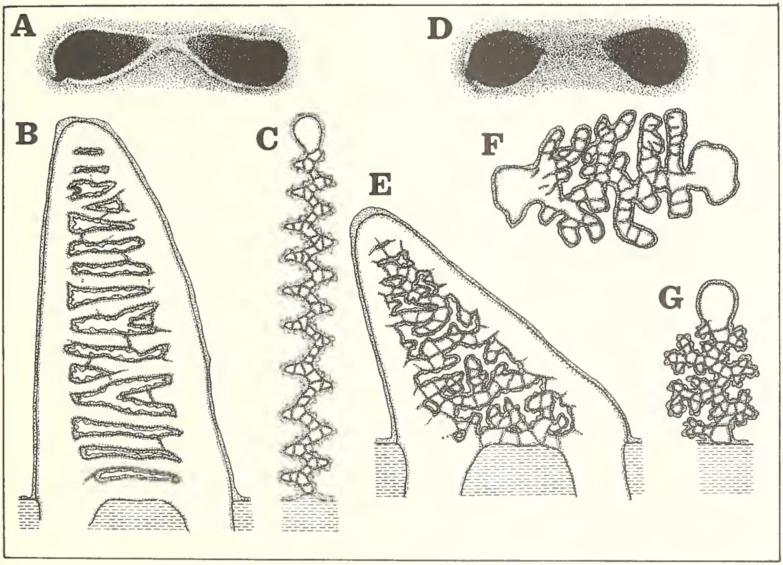


TEXT-FIG. 3. Aboral respiratory tube foot and ampulla of *Echinolampas crassa*. A, longitudinal section; B, sagittal section; C, D, detailed morphology as indicated; E, associated anisopore.

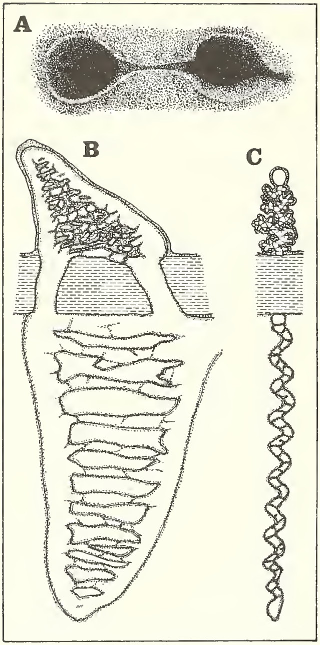
In all these respiratory tube feet a single layer of fine muscle fibres is present in the walls of the two main channels and fine contractile fibres are also sparsely distributed throughout the central region. A circular connective tissue layer is present but is usually thin so that the combined thickness of the muscle and connective tissue layers is never more than a few μm. The epithelial layers are usually just one cell thick and in the ectoderm it is typical to find groups of nuclei clustered together. The endothelial cells, lining the passageways of the central area, are heavily ciliated. The ectoderm is also well ciliated.

The associated ampulla is extremely broad and flat. The walls of the ampulla have no more than a thin membrane of connective tissue and few, if any, contractile fibres. The narrow lumen of the ampulla is crossed by epithelial septa with elongate nuclei, partitioning the lumen into a large number of passageways, much as in the respiratory tube feet (text-fig. 2). These ampullae may be linked with one another by thin, connective-tissue strands which originate from the inner edge of the ampullae. In *E. cordatum* and *S. raschi*, the ampullae were found to have a broad, central, corrugated area, crossed by septa and linking the two major channels which run the length of each ampulla (text-fig. 5).

Suckered tube feet (text-figs. 6-8). Suckered tube feet which resemble those of regular echinoids were found only in the holectypoid *Echinoneus cyclostomus*. This species has both oral and aboral suckered tube feet (text-fig. 6). The stem of the tube foot has both circular and longitudinal connective tissue fibres and there is also a layer of stem retractor muscle fibres. A short septum extends for about a quarter of the length of the lumen from the interporal partition. The sucking disc is composed of an outer ring of dense epithelial cells, forming a sensory pad, and a central region with muscle fibres running from the cuticle to the connective tissue layer. There are clumps of cells, found largely beneath the rosette, giving rise to ducts which can be traced to the disc surface. These are presumably secretory in function. Levator muscle fibres run from the centre of the disc to the rosette. The rosette and frame in a tube foot of *Echinoneus* have been illustrated by Lovén (1883). Oral and aboral tube feet of *Echinoneus* are similar in structure but differ in size, the diameter of the disc in oral tube feet being around 150 μm compared with 120 μm for aboral tube feet. In some aboral tube feet the skeletal framework of the disc may be so reduced as to be almost lost. These tube feet still retain their suction power since the disc and levator muscle fibres are just as well developed as they are in oral tube feet.



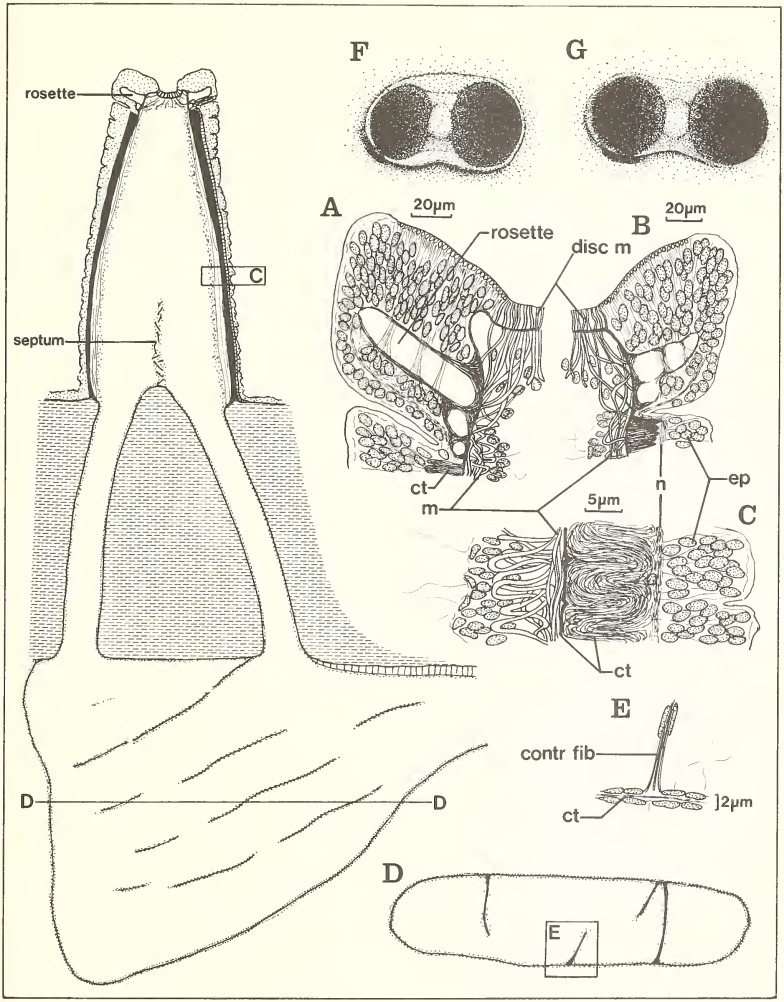
TEXT-FIG. 4. A–C, aboral respiratory tube foot and isopore of *Brissopsis lyrifera*: A, associated isopore; B, longitudinal section; C, sagittal section. D–G, aboral respiratory tube foot and isopore of *Spatangus raschi*: D, associated isopore; E, longitudinal section; F, transverse section through tube foot; G, sagittal section through tube foot.



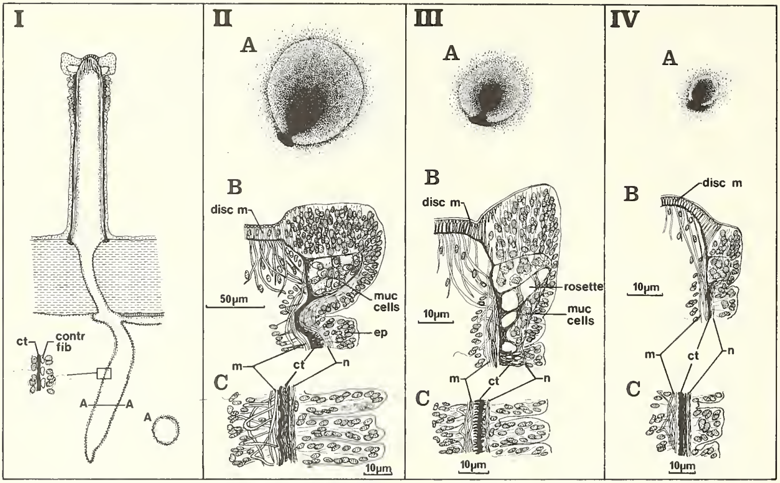
TEXT-FIG. 5. Aboral respiratory tube foot and ampulla of *Echinocardium cordatum*. A, internal plate surface showing the conjugate furrow between pores; B, longitudinal section; C, sagittal section.

The sucking disc in *Echinoneus* is intermediate in character between the discs of regular echinoids and the sucking discs of cassiduloids and clypeasteroids. On the one hand the disc has many of the features, including a frame and rosette, that are found in the discs of regular echinoids. Yet, as in cassiduloids and clypeasteroids there are disc muscles lying outside the connective tissue layer, a condition only met with in certain cidaroids amongst regular echinoids (Nichols 1961; Smith 1978*b*). The ampullae of *Echinoneus* are also intermediate in their characteristics. They are rather squat and relatively broad and the lumen is crossed by only three or four septa. Contractile fibres are associated with the septa and they are also present in the walls of the ampulla.

In other groups of irregulars, suckered tube feet tend to be much smaller and possess less well-developed rosettes. In the cassiduloids that were examined the oral tube feet were all found to have a terminal sucking disc (text-fig. 7). The stem follows the normal pattern found in echinoid tube feet, with both circular and longitudinal connective tissue fibres as well as muscle fibres. In the disc there is a small rosette but no frame. Both levator and disc muscle fibres are present and there is an outer ring of dense epithelial cells which form a sensory pad. Between the sensory pad and the disc muscle fibres there is a loose mesh of cells amongst which ducts can be seen running to the surface of the disc. The ampulla is always elongate and cylindrical. The lumen of the ampulla is not crossed by septa. Contractile fibres are readily apparent in the walls of the ampulla and these run circularly and branch to interconnect with one another.



TEXT-FIG. 6. Tube foot and ampulla of *Echinoneus cyclostomus*. A, longitudinal half-section of the sucking disc of an oral tube foot; B, longitudinal half-section of the sucking disc of an aboral tube foot; C, longitudinal section of part of the stem of an oral tube foot; D, E, structure of the ampulla, as illustrated; F, partitioned isopore of the oral surface; G, partitioned isopore of the aboral surface.

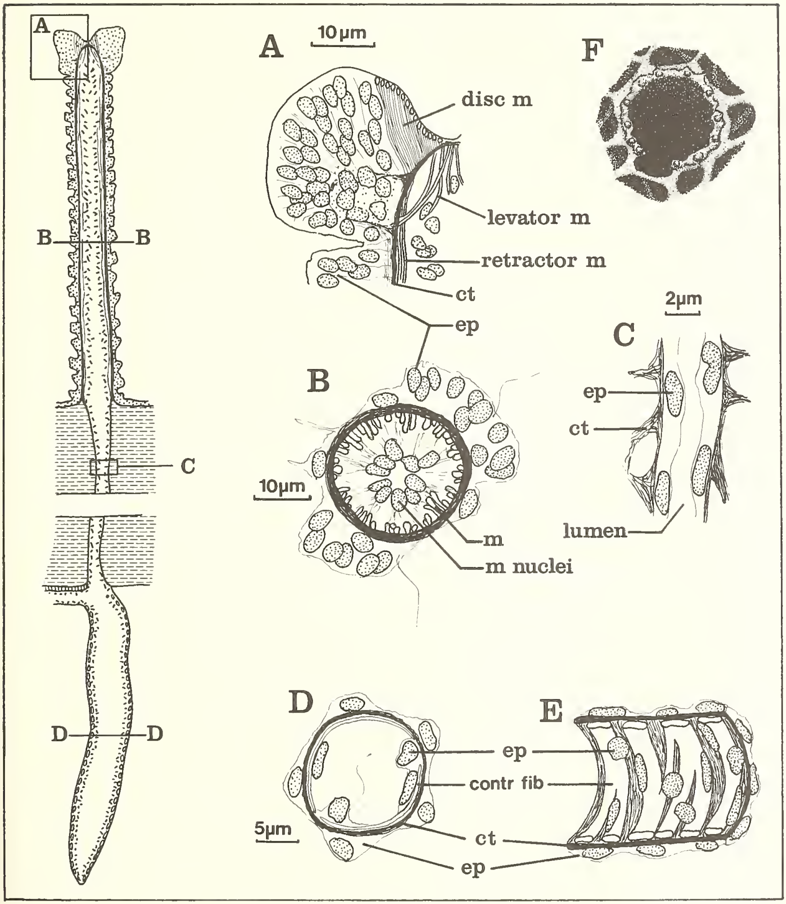


TEXT-FIG. 7. Suckered tube feet of cassiduloids. I, general longitudinal section. II, phyllode tube foot of *Echinolampas crassa*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. III, phyllode tube foot of *Cassidulus cariboearum*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. IV, ambital tube foot of *Apatopygus recens*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. The difference in disc shape is due to the state of contraction of the levator and disc muscles.

The ambital tube feet of cassiduloids are relatively smaller but are similar in structure (text-fig. 7). The disc muscle fibres are well developed and the rosette is commonly reduced to a circle of spicules. The ampullae are again cylindrical and have prominent contractile fibres.

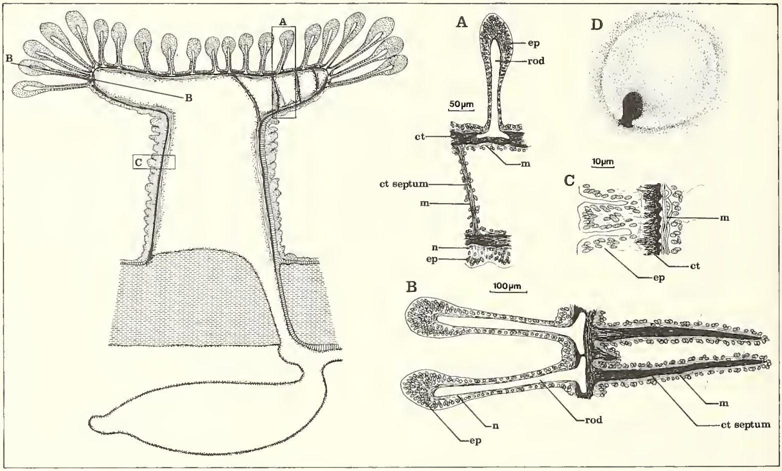
The smallest suckered tube feet that were found in this survey are the so-called 'accessory' tube feet of clypeasteroids. These are very similar to the ambital tube feet of cassiduloids. The detailed histology of these tube feet in *Echinocyamus* has been provided by Nichols (1959*c*) and other suckered tube feet of clypeasteroids were found to differ little in their structure. The morphology of the suckered tube feet of *Echinodiscus bisperforatus* is given in text-fig. 8. The terminal disc has well-developed, disc muscle fibres and levator muscles. The rosette, in *Clypeaster*, is reduced to a small circular element and in sand dollars there is only a ring of spicules (Durham 1955). The ampulla is simple and cylindrical with prominent contractile elements which run circularly around the walls. In the clypeasteroids which have a system of food grooves, it is common to find that those tube feet lying in, or adjacent to, a food groove are squat with large heads and fewer disc and stem muscle fibres. These tube feet possess a thickened nerve plexus and epithelial pad which includes mucous-secretory cells, according to Chia (1969). These tube feet are likely to be much less active than the more slender and elongate tube feet of the rest of the ambulacral surface. The variation in size of these suckered tube feet has recently been pointed out by Phelan (1977).

There are a number of published accounts concerning the activity of suckered tube feet and it appears that they are primarily used in feeding and burial activities. Rose (1978) reports that, in *Echinoneus*, oral tube feet collect grains of substrate and pass them towards the peristome and into



TEXT-FIG. 8. Suckered tube foot of *Echinodiscus bisperforatus*. A–D, detailed morphology as indicated; E, diagrammatic cut-out section of the wall of the ampulla to show the interbranching of the circular contractile fibres; F, associated micro-unipore.

the mouth. Oral tube feet are also used to adhere to rocks and large coral fragments, possibly for stability. Tube feet are also involved in passing grains aborally during burial where the aboral tube feet hold them in position. The life styles of three species of cassiduloid have recently been published (Higgins 1974; Thum and Allen 1976; Gladfelter 1978) and it is known that oral tube feet selectively collect and transfer sediment grains to the peristome. It is likely that ambital tube feet may help to pass sediment grains aborally during burial but this has not been reported. In the clypeasteroid *Echinocyamus* tube feet again assist in burial by passing grains aborally and holding them there (Nichols 1959*c*) but apparently take little part in feeding activities. However, in sand dollars, such as *Leodia* (Goodbody 1960), *Mellita* (Bell and Frey 1969), and *Dendraster* (Chia 1969; Timko 1976) tube feet appear to be primarily concerned with the capture of particles and their transference to the mucous-rope which lies in the food groove. The large and squat tube feet of the floor of the food grooves are sites of mucus production and their activity moves the mucous-rope towards the peristome. These tube feet also play an active role in the selection and rejection of particles at the Y junctions of food grooves (Timko 1976).



TEXT-FIG. 9. Phyllode tube foot of *Spatangus raschi*. A–C, detailed morphology as indicated; B, part of a transverse section across half of the disc in the plane BB; D, the associated unipore.

Buccal and phyllode tube feet (text-fig. 9). In the cassiduloids, tube feet of the oral surface are all suckered and have more or less the same structure, described above. In a number of clypeasteroids, however, ten large tube feet are found surrounding the peristome and these are known as buccal tube feet. The histology of buccal tube feet of *Echinocyamus* has been detailed by Nichols (1959*c*). The buccal tube feet of sand dollars appear to be similar in structure to those of *Echinocyamus* but much difficulty was encountered in serial sectioning these tube feet due to the large number of adhering sand grains. In *Echinocyamus* buccal tube feet are largely sensory in function and actively probe the substrate (Nichols 1959*c*). In *Dendraster*, however, these tube feet transfer the mucous feeding-rope into the peristome (Chia 1969).

It is in the holasteroids and spatangoids that highly modified phyllode tube feet are found. The structure of these tube feet is remarkably uniform so that tube feet from the phyllode of the holasteroid *Urechinus naresianus* are more or less identical to those of spatangoids such as *S. raschi* (text-fig. 9) or *Echinocardium cordatum* (Nichols 1959*a*). These tube feet, when contracted, are very squat and possess a broad disc which is covered in papillae. The stem has the typical morphology found in most tube feet (text-fig. 9C) with only a thin layer of retractor muscle fibres. These muscle fibres attach to the periphery of the isopore or unipore leaving a large periporal area, which is covered by a single layer of squamous epithelial cells which are sparsely ciliated. The lumen of the tube foot extends well into the disc but it is here partitioned by a large number of septa, composed of connective tissue fibres, which connect the upper and lower surfaces of the disc. These septa radiate out to the margin of the disc lumen from a central position. A skeletal rod forms the core to each papilla and each has its base embedded within the connective tissue layer of the disc. The stem of each papilla has a single layer of epithelial cells which, on the underside of the skeletal rod, is underlain by nervous tissue. The tip of the papilla is swollen and is composed of a densely nucleated pad of epithelium in which Nichols (1959*a*) found abundant mucous glands. The papillae, which occur over the whole surface of the disc, are largest at the periphery and decrease in size towards the centre of the disc. There is no apparent correlation between the positioning of the radial septa of the lumen and the positioning of the papillae.

Although levator muscle fibres are wanting there are numerous muscle fibres in the lumen of the disc. Stem retractor muscle fibres appear to continue into the disc, running along the lower floor of the lumen to the periphery. Muscle fibres also run obliquely up the radial septa connecting the lower and upper surfaces of the lumen. There are also muscle fibres that run radially across the upper surface of the lumen.

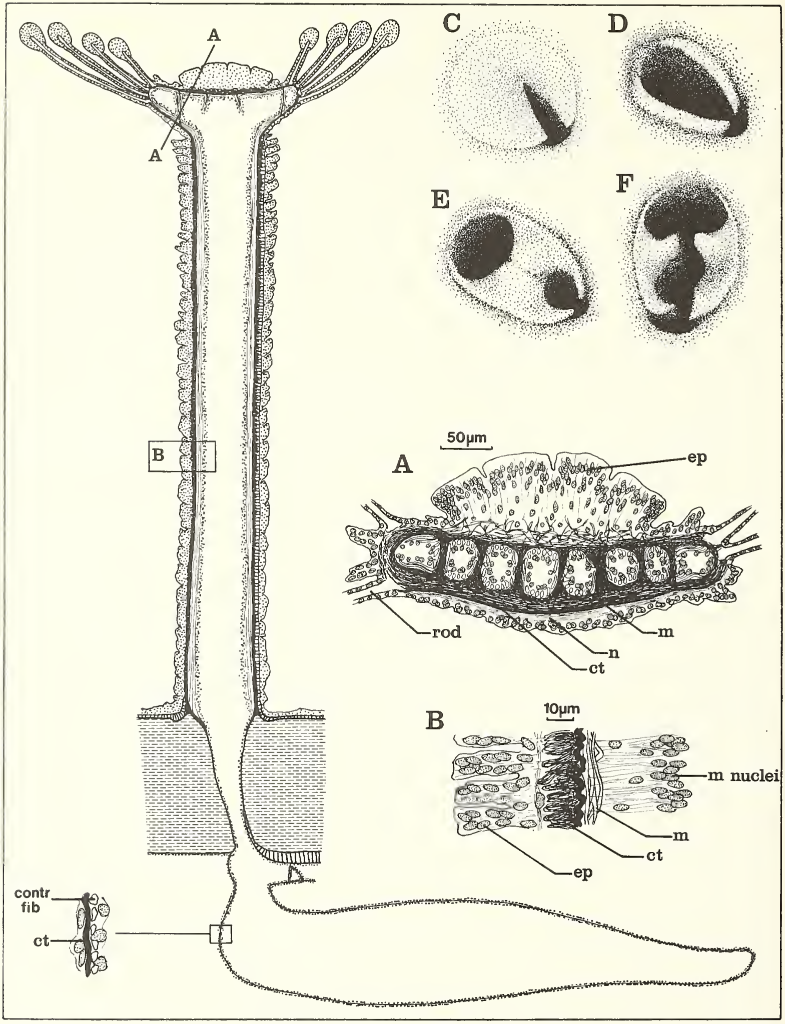
The ampulla is a large bulbous tube lacking septa. Both the connective tissue layer and the contractile fibre layer are well developed, their combined thickness being about 2 to 5 μm. As in other cylindrical ampullae, these contractile fibres run circularly and interconnect with one another.

Lovén (1883) found only three spatangoids in which the phyllode tube feet differed in appearance from that described here. In all three (*Aceste*, *Palaeostoma*, *Palaeotropus*) the tube feet differed in possessing papillae only around the margins of the disc, an arrangement typical of sub-anal tube feet.

The phyllode tube feet of a number of species have been shown to function primarily in the gathering and transference of quantities of substrate into the peristome (Nichols 1959*b*; Chesher 1963, 1968, 1969).

Funnel building tube feet: sub-anal tube feet (text-fig. 10). In spatangoids, the tube feet which originate from within the sub-anal fasciole are highly specialized. These tube feet have a long and slender stem which terminates in a disc bearing papillae (text-fig. 10). In *Brissopsis lyrifera*, *S. raschi*, *Metalia sternalis*, and *E. pennatifidum* the disc has a broad, central pad of epithelial tissue, and papillae are found only around the rim of the disc. The papillae are arranged into from two to four irregular rows, with the largest papillae being situated furthest from the centre. Depending upon the size of the disc, there are between 50 and 120 or so papillae to each tube foot. The skeletal rods of the papillae do not appear to be bound into the connective tissue layers of the disc but simply rest in the overlying epithelium, as noted by Nichols (1959*a*). The lumen extends into the disc and radial septa are present. The muscle and septal arrangement is similar to that described previously for phyllode tube feet. The central pad appears to be well endowed with mucous glands and the underlying connective tissue is loosely packed and either contains spicules or small plates (illustrated by Lovén 1883). The tube foot stem and its ampulla (text-fig. 10) are standard in their morphology.

The sub-anal tube feet of *E. cordatum* differ from those of other spatangoids in that the disc has papillae which cover the whole of the surface of the disc. This disc is, however, very much smaller than the disc of phyllode tube feet. Nichols (1959*a*) reports finding one tube foot within the sub-anal fasciole which corresponds with the more typical structure, described above, but this is an unusual occurrence.



TEXT-FIG. 10. Sub-anal tube foot of *Brissopsis lyrifera*. A, section across the disc in the plane AA; B, longitudinal section of part of the stem; C, the associated unipore; D, sub-anal unipore of *Echinocardium cordatum*; E, sub-anal isopore of *Metalia dichrana*; F, sub-anal constricted unipore in *Protenaster australis*.

The sub-anal tube feet have been shown to construct and maintain a sanitary drain in the sediment (Nichols 1959*b*; Chesher 1968). These tube feet excavate particles from the back wall and drop them by the sub-anal tuft of spines which then incorporates them into the burrow wall. They also plaster mucus along the walls of the tunnel.

Funnel-building tube feet: aboral ambulacrum III tube feet (text-fig. 11). The least specialized dorsal, funnel-building tube feet were found in *B. lyrifera* and *Hemiaster expurgitus* (text-fig. 11I). These possess a broad, circular disc which, in *Brissopsis*, is scalloped at the margins. The disc is supported upon a short and relatively squat stem of standard morphology. The disc incorporates a ring of flattened rods which form a rosette. There are ten or eleven such rods in *Hemiaster* and fifteen to eighteen rods in *Brissopsis*. These rods do not continue to the centre but leave an uncalcified circle at the centre of the disc. (Lovén (1883) reported finding a single specimen of *B. lyrifera* in which there was a thin central plate.) In the inner part of the rosette the rods abut on one another but towards the distal end each becomes separate (text-fig. 11I). The nerve ring, which lies beneath the rosette at the top of the stem, gives off tracts of fibres which pass to the upper surface of the disc at the point where adjacent rods diverge. The surface of the disc has a broad pad of epithelial tissue with what appear to be numerous mucous glands. Towards the tip of each rod the epithelial layer swells slightly and, in *Brissopsis*, the margin is indented between each rod. The densely nucleated, epithelial pad at the tip of each rod bears some similarity to the epithelial pad at the tip of the papillae. Levator muscle fibres are present and these run from the connective tissue at the centre of the disc to the rosette. The associated ampulla is cylindrical with prominent contractile fibres and no septa. Lovén (1883) found a rather similar skeletal arrangement in the dorsal, funnel-building tube feet of a number of other species. In some the disc is circular, in others it is deeply indented but all have a similar rosette. This appears to be the most common type of dorsal, funnel-building tube foot in the spatangoids.

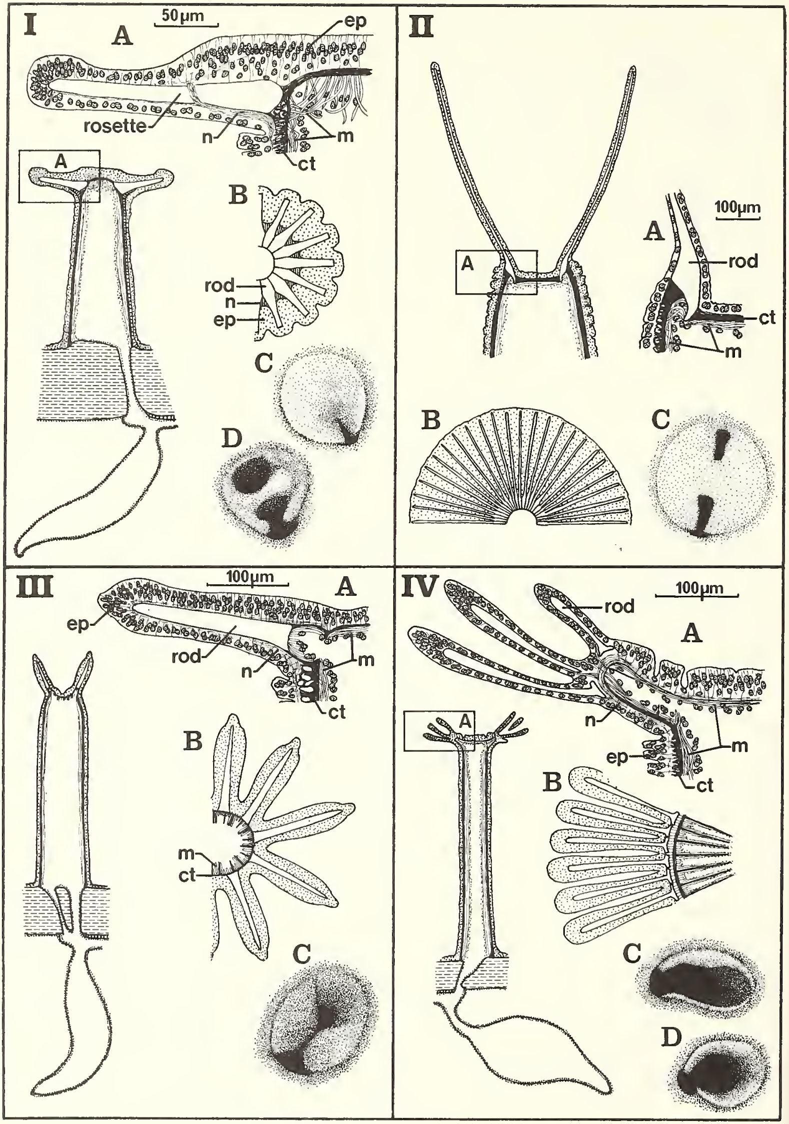
In *Aeropsis rostrata* the dorsal, funnel-building tube feet are very large and the rods of the disc are very long and thin (text-fig. 11II). Each rod enlarges and becomes keeled proximally, where it comes to abut on to neighbouring rods. Along the rest of their length the rods are connected by a connective tissue sheet to produce a webbed disc. The surface of the disc is covered with a thin layer of epithelial cells. Muscle fibres run between rods, across the centre of the disc, and also from the hooked proximal end of each rod to the stem. The disc can therefore be opened to present a broad, circular surface or can be closed to produce a flat, fan-shaped array. The arrangement of rods is only superficially similar to the arrangement found in the 'umbrella' tube feet of *Micropyga*.

In the dorsal, funnel-building tube feet of *E. pennatifidum* the disc morphology is rather different. The disc has a ring of nine or ten acicular rods which are independent of one another. Each terminates in the connective tissue layer of the disc (text-fig. 11III). The lumen of the tube foot enters the disc, and short radiating septa of connective tissue cross the lumen of the disc. Each element forms the core to a papilla. The papillae are composed of dense epithelial tissue. Muscle fibre arrangement in the lumen of the disc is similar to that described for phyllode tube feet.

The most highly modified dorsal, funnel-building tube feet are found in *E. cordatum* (text-fig. 11IV). The disc has a central pad of epithelial cells and mucous glands surrounded by a marginally situated ring of papillae, irregularly arranged into three or four rows. The detailed histology of these tube feet has been given by Nichols (1959*a*). They are very similar to the sub-anal tube feet of other spatangoids, described previously, but differ in commonly possessing a massive, bipolar spicule immediately beneath the disc.

Dorsal, funnel-building tube feet function in much the same way as do sub-anal tube feet in that they excavate sediment from an apical funnel and they plaster mucus on to the walls of this funnel. In addition the tube feet of *E. cordatum* are known to rake particles from the sediment/water interface and pull them down the funnel (Robertson 1871; Buchanan 1966). Similar activity has never been observed in *B. alta* or *B. atlantica* (Chesher 1968). The function of the tube feet of *Aeropsis*, with their webbed disc, is unknown.

In a number of spatangoids, the dorsal tube feet of ambulacrum III are discless and terminate in a sensory pad. These sensory tube feet have been described above.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PORE MORPHOLOGY AND DISTRIBUTION

Isopores

Pore pairs, where both pores are approximately the same size and shape, can be separated into a number of categories according to the pore shape, the size and position of the neural canal, and the morphology of the interporal partition.

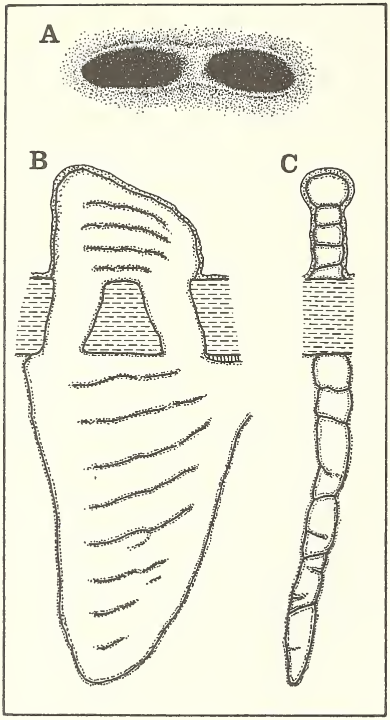
1. *Conjugate isopores* (Pl. 1, figs. 1–3; text-fig. 2). The two pores each have a rounded outline and are similar in size. The major axis of the isopore parallels the adoral plate suture and, in some cases, comes to overlie this suture. The neural canal is feebly developed and may be absent. Where present, it lies meso-adorally in the perradial pore. The interporal partition is broad and at least equal in breadth to the diameter of one pore. The interporal partition is crossed by a narrow furrow which links the pores.

Conjugate isopores were found aborally in a number of cassiduloids and in some clypeasteroids and spatangoids. They have also been found aborally in cidaroids and arbacioids (Smith 1978*b*). In all groups of irregular echinoids these isopores were never found to possess any specialized attachment area. In those species where the histology of the associated tube foot was examined (*Apatopygus recens*, *Cassidulus cariboearum*, *Echinocyamus pusillus*, and *Echinodiscus bisperforatus*), the tube foot was found to be specialized for gaseous exchange. A central, partitioned region is present in all tube feet and this is unbranched. In *Apatopygus* and *Cassidulus* the tube foot is relatively tall and narrow but in *Echinodiscus*, where the interporal area is very much broader, the tube foot is relatively short. These tube feet possess a small sensory tip which is skewed towards the adradial side. The walls of the central, partitioned region attach to the side walls of the interporal furrow.

2. *Elongate isopores* (Pl. 1, figs. 4, 5; text-figs. 4, 12). The isopore is long and narrow and lies parallel to the adoral ambulacral suture. Both pores are equally elongate along their common axis and each may taper slightly towards the interporal partition. The neural canal is small or absent. The interporal partition is usually rather narrow, though it may be quite broad in some cases, and is crossed by an area of raised stereom. This area links the two pores and may continue laterally, forming a narrow rim both adoral and adapical to each pore. The symmetrical taper of both pores and the narrow breadth of the raised band crossing the interporal partition give this isopore a waisted appearance.

Elongate isopores were found only in spatangoids and in fossil holasteroids. The histology of the associated tube foot was examined in only three species. In *H. expurgitus* and *Palaeostoma mirabile* the tube feet are small and each has a central, partitioned region which is unbranched (text-fig. 12). In *B. lyrifera* the central, partitioned region has side branches (text-fig. 4). The walls of the central, partitioned region attach to the margins of the raised interporal area and to the lateral rim of the pores. The morphology of tube feet associated with elongate isopores that possess a broad interporal area has not been investigated.

TEXT-FIG. 11. Longitudinal sections through dorsal funnel-building tube feet of spatangoids. I, *Brissopsis lyrifera*: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show the rosette; C, associated unipore; D, partitioned isopore associated with a similar tube foot in *Hemiaster expurgitus*. II, *Aeropsis rostrata*; distal part of tube foot: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show the rosette; C, associated isopore. III, *Echinocardium pennatifidum*: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show arrangement of rods and small development of septa; C, associated unipore. IV, *E. cordatum*: A, longitudinal half-section across the disc; B, transverse segment of the disc; C, associated unipore from outer row; D, associated unipore from inner row.



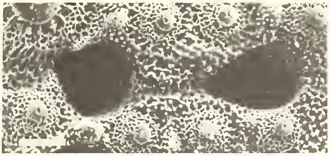
TEXT-FIG. 12. Aboral respiratory tube foot and ampulla of *Hemiaster expurgitus*. A, associated isopore; B, longitudinal section; C, sagittal section.

EXPLANATION OF PLATE 1

Figs. 1–8. *Petal isopores*. Top of photomicrograph adapical unless otherwise stated. 1, *Apatopygus recens* (Milne-Edwards). Conjugate isopore from aboral ambulacrum II. Top of photomicrograph adoral. 2, *Clypeaster rosaceus* (Linnaeus). Conjugate isopore from aboral ambulacrum II. 3, stereoview of conjugate isopores of *Echinocyamus pusillus* (Muller) from aboral ambulacrum IV. 4, stereoview of an elongate isopore of *Brissopsis lyrifera* (Forbes) from aboral ambulacrum II. 5, *Hemiaster expurgitus* Lovén. Elongate isopore from aboral ambulacrum IV. 6, *Clypeaster rarispina* de Meijere. Isopores with a flush interporal partition from aboral ambulacrum III. 7, *Paramaretia peloria* (Clark). Isopore with a flush interporal partition from aboral ambulacrum II. 8, *Echinocardium cordatum* (Pennant). Isopore with a flush interporal partition from aboral ambulacrum V.

Scale bar in figs. 1, 3, 5 = 100 μm; 4, 6, 7 = 200 μm; 8 = 400 μm; 2 = 1 mm.

PLATE 1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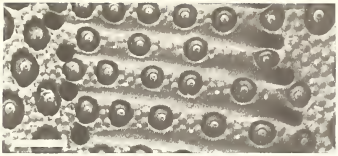
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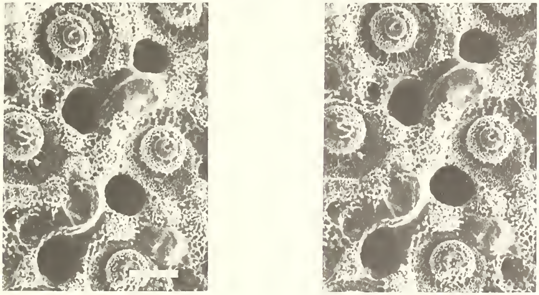
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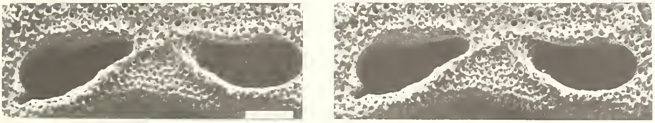
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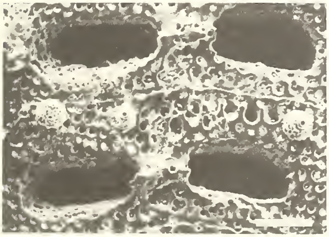
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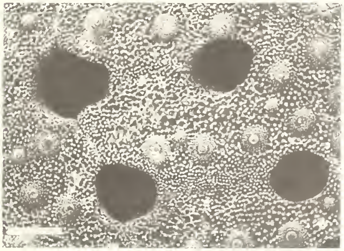
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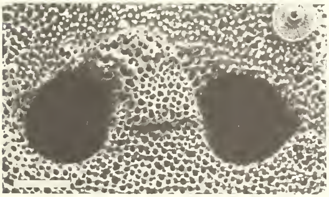
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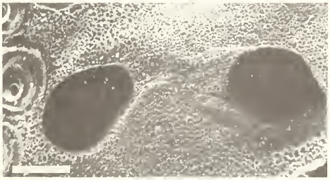
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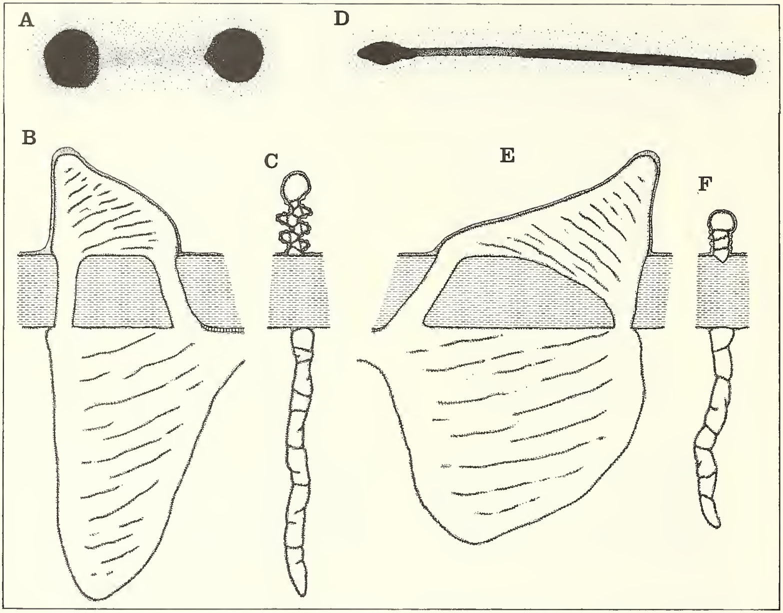
SMITH, Echinoid isopores



TEXT-FIG. 13. A–C, aboral respiratory tube foot and ampulla of *Clypeaster rarispina*: A, associated isopore with flush interporal partition; B, longitudinal section; C, sagittal section. D–F, aboral respiratory tube foot and ampulla of *Mellita quinquiesperforata*: D, associated conjugate anisopore; E, longitudinal section; F, sagittal section.

3. *Isopores with a flush interporal partition* (Pl. 1, figs. 6–8; text-figs. 4, 13). The pores are similar in size and may be circular or pear-shaped. If pear-shaped, each pore tapers towards the interporal partition and the major axes of each are not parallel but converge obliquely in an adapical direction. The relatively broad interporal partition lies more or less flush with the rest of the plate surface. The neural canal is typically feebly developed or is absent altogether. The interporal area is crossed by a band of stereom of different appearance from stereom of the surrounding plate surface (Pl. 1, fig. 7). In some cases this band is linear and is centrally positioned on the interporal partition. In others, the band lies adapical on the interporal partition and is gently curved. It also narrows considerably towards the centre of the interporal area.

Of the species examined only *Clypeaster rarispina* was found to have isopores with a flush interporal partition with a centrally positioned stereom band. These occur aborally and the associated tube feet have a central, partitioned area which has small side branches (text-fig. 13). Isopores that are adapically arched form the petals in a number of species of spatangoid. In *Echinocardium cordatum* and *Spatangus raschi*, the associated tube foot has a central, partitioned region with numerous side-branches, which may themselves be branched (text-fig. 4). The tube foot is skewed adradially. In both types, the central, partitioned region of the tube foot attaches on to the band of modified stereom which crosses the interporal partition.

4. *Partitioned isopores.* The term partitioned isopore encompasses all those isopores in which the two pores are not joined to one another by a furrow, a ridge, or a distinct stereom band, as described above. Partitioned isopores are separated by a well-defined interporal partition and possess a clear neural canal. An important subdivision can be made based on the positioning of the neural canal and this reflects a difference in the structure of the associated tube foot/ampulla system. The two groups of partitioned isopores are those with an axially positioned neural canal and those with a laterally positioned neural canal. The functional significance of this difference will be discussed in a later section.

Partitioned isopores with a laterally positioned neural canal (Pl. 2, figs. 1–3; text-fig. 6). These are the typical isopores present in all groups of regular echinoids and they have been grouped by Smith (1978*b*) according to the breadth of their attachment area. The major axis of these isopores lies parallel or only slightly oblique to the adoral suture of the plate. The neural canal lies in a meso-ventral position on the perradial pore and is always in contact with the adradial suture.

Partitioned isopores with a laterally positioned neural canal are not common in irregular echinoids but do occur in two groups of primitive irregulars, the pygasteroids (Smith 1978*a*) and the holectypoids. Both oral and aboral tube feet of the Recent holectypoid *Echinoneus cyclostomus* terminate in a sucking disc, described previously (text-fig. 6). The associated isopores have a narrow attachment area which is slightly better defined in oral isopores than in aboral isopores (Pl. 2, figs. 1, 3). Fossil holectypoids, such as *Holectypus depressus* (Leske) (Pl. 2, fig. 2) have a similar pore morphology.

This type of partitioned isopore was observed in only two other irregular echinoids that were examined. In both the Jurassic galeropygoid *Galeropygus agariciformis* (Forbes) and in the Recent spatangoid *Genicopatagus affinis* Agassiz, a single row of P1-type isopores occurs in each aboral ambulacral column (excluding the anterior ambulacrum of *Genicopatagus*). These presumably bear thin-walled, suckerless tube feet as in regular echinoids.

Partitioned isopores with an axially positioned neural canal (Pl. 2, figs. 5, 7; Pl. 3, fig. 1; text-figs. 10, 11, 14). In these, the neural canal is positioned so as to lie on the major axis of the isopore in alignment with the two pores. In the primitive condition, the isopore is orientated so that the adradial pore lies adapical to the perradial pore, whilst the neural canal typically abuts on to the adoral plate suture. Where 'plate-crushing' occurs, packing the isopores close together, the adradial pore returns to an adradial position so that the major axis of the pore parallels the adoral plate suture. The neural canal retains its axial position, sometimes maintaining contact with the adoral plate suture but, more often than not, becoming separated from the suture. Unlike the majority of partitioned isopores with a laterally positioned neural canal, the two pores show little divergence as they pass inwards through the plate. Indeed many isopores have slightly convergent pores which may coalesce to produce a single pore at the inner surface of the plate. On the external surface the interporal partition may be raised, planar, or even depressed. A distinct attachment area is commonly, though not always developed around the pores.

Partitioned isopores with an axially positioned neural canal are found in many groups of echinoids. The peristomial tube feet of many regular echinoids are associated with this type of isopore. The early galeropygoids and cassiduloids, such as *Galeropygus* and *Clypeus* possess oral and ambital isopores with this structure (Pl. 2, fig. 7) as do early disasteroids such as *Pygomalus*. Finally these isopores are often found in spatangoids and holasteroids, typically in the sub-anal region or dorsally in the anterior ambulacrum: they may also be found surrounding the peristome as in *Echinocorys*, *Micraster*, and *Infulaster*.

It is hoped to be able to present the results of a study on the morphology of peristomial tube feet and their pores elsewhere. The following discussion will therefore be limited largely to the spatangoids where the morphology of tube feet in a large number of species is known, some having been examined by the author, others described by Lovén (1883).

Sub-anal tube feet are remarkably uniform in their construction. Although many are associated with unipores, six of the species examined have sub-anal isopores with axially positioned neural canals. Of these, four (*Brissaster fragilis* (Düben and Koren), *Brissopsis luzonica* Gray, *Metalia sternalis* (Lamarck), and *M. dichrana* Clark) have sub-anal tube feet similar in external appearance to those of *B. lyrifera* (text-fig. 10). On the other hand, *Breynia australasia* (Leach) has, according to Lovén (1883), a disc covered in papillae, resembling the sub-anal tube feet of *Echinocardium cordatum*. Tube feet of the sixth species, *Paraster compactus* Koehler, were not examined.

Dorsal, funnel-building tube feet of ambulacrum III are more variable in their structure and are often associated with this type of isopore. In *B. australasia* and *P. floridiensis* Kier and Grant, the dorsal tube feet (illustrated by Lovén 1883, and Chesher 1966, respectively) have a disc bearing only a few large papillae and are similar in external appearance, to those of *E. pennatifidum* (text-fig. 11III). Others, such as *Hemiaster expurgitus* and *Palaeostoma mirabile*, have tube feet which terminate in a flat disc with a circular or scalloped outline and with a rosette composed of radiating rods, much like *Brissopsis lyrifera* (text-fig. 11I). Dorsal, funnel-building tube feet of *Moira atropos* (Lamarck) (illustrated by Chesher 1963), *Schizaster canaliferus* (Lamarck), and *Metalia sternalis* (Lamarck) have a similar rosette of radiating rods but deep indentations of the margin between each rod give the disc a fingered appearance. Tube feet of *Paraster compactus* and *P. doderleini* Chesher have discs with long and slender rods joined by a membrane. This is taken to an extreme in the dorsal tube feet of *Aeropsis rostrata* (text-fig. 11II). All these types of tube feet are found associated with partitioned isopores. Although there is some variation in the detailed morphology of these isopores, it is not possible to identify the nature of the tube foot disc from the structure of the isopore.

Phyllode pores in *P. compactus* and occasionally in the holasteroid *Urechinus wyvilli* Agassiz are this type of partitioned isopore and in these species the associated tube feet have a disc covered in papillae. Finally, because of their size, no survey of the minute ambital pores of spatangoids was carried out at the light microscope level. In those spatangoids examined with the SEM all ambital tube feet (which are sensory in function) were found to be associated with unipores. Lovén (1883), however, gives illustrations of some minute isopores which he found ambitally in certain species. The very small size of these isopores and the probability of their possessing little or no attachment area should make these readily distinguishable from larger isopores which support tube feet that possess a terminal disc.

From the preceding discussion it is obvious that partitioned isopores are associated with a number of tube feet of differing structure and function. Some correlation can, however, be drawn between the structure of the isopore and the morphology of the tube foot/ampulla system.

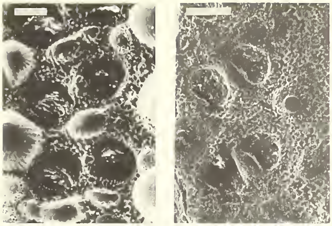
(i) All tube feet found in association with partitioned isopores have cylindrical stems and are not especially modified for gaseous exchange.

(ii) The ampullae found with partitioned isopores with a laterally positioned neural canal are broad and flat and are partitioned by septa. The ampullae which occur with partitioned isopores where the neural canal is axially placed are cylindrical, with a well-developed contractile fibre layer and with no septa crossing the lumen.

EXPLANATION OF PLATE 2

Figs. 1–7. Top of photomicrographs adapical unless otherwise stated. 1, stereoview of two partitioned isopores with laterally positioned neural canals from the aboral ambulacrum III of *Echinoneus cyclostomus* Clark. 2, stereoview of two partitioned isopores with laterally positioned neural canals from the aboral ambulacrum IV of *Holectypus depressus* (Leske). 3, *E. cyclostomus* Clark. Oral partitioned isopore with a laterally positioned neural canal. 4, *Echinocardium cordatum* (Pennant). Unipore with an extensive periporal area from the phyllode. 5, stereoview of three partitioned isopores with axially positioned neural canals from aboral ambulacrum III of *Moira atropos* (Lamarck). 6, stereoview of a broad-rimmed unipore present adapically in ambulacrum III of *Pourtalesia miranda* Agassiz. 7, isopore with an axially positioned neural canal from the phyllodes of *Clypeus* sp. Adapical to right.

Scale bar in figs. 1–3, 6, 7 = 100 μm; 5 = 200 μm; 4 = 400 μm.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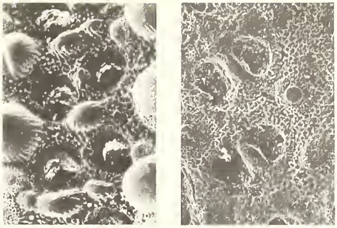
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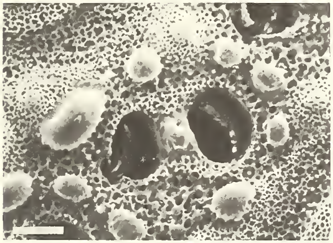
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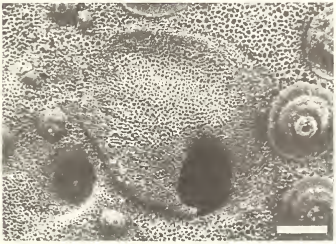
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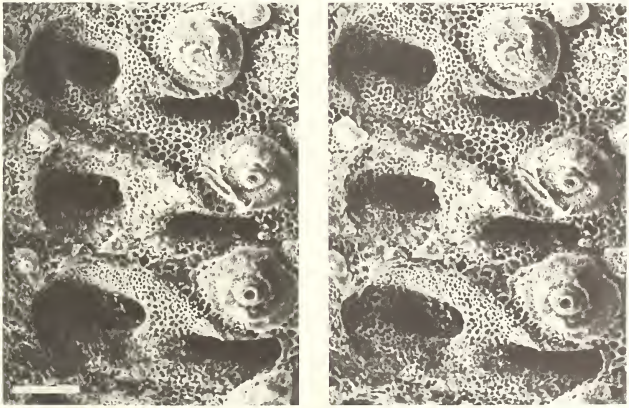
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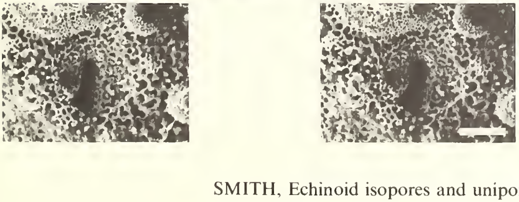
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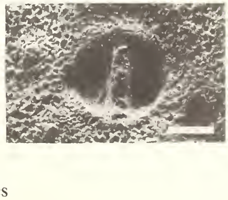
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SMITH, Echinoid isopores and unipores

(iii) Most tube feet found with partitioned isopores have some form of terminal disc. Those that do not can often be identified from the feeble development or complete absence of a specialized attachment area to the isopore. In spatangoids and holasteroids these isopores are relatively very small.

(iv) Partitioned isopores with a laterally positioned neural canal and an obvious attachment area are associated with tube feet that possess a terminal sucking disc. Partitioned isopores with an axially positioned neural canal, found in holasteroids and spatangoids, have tube feet whose flat or penicillate discs rely on mucus secretion for their adhesiveness. Similar isopores found in extinct members of the Cassiduloidea probably supported tube feet with sucking discs like those of their living relatives.

Anisopores

Ambulacral pore pairs, where the pores differ markedly in size and shape, are much more restricted in occurrence than either isopores or unipores. They are separated here into two groups, conjugate anisopores and non-conjugate anisopores.

1. *Conjugate anisopores* (Pl. 3, figs. 2–4; text-figs. 3, 13). These anisopores are extremely elongate and parallel, or even overlie, the adoral plate suture. The perradial pore is typically small and circular in outline with no more than a faint trace of a neural canal. The adradial pore is very elongate and is separated from the perradial pore by an often quite broad interporal partition. The two pores are linked by a furrow which crosses the interporal partition. The adradial pore tapers towards this furrow. In *Dendraster excentricus*, the adradial pore is partitioned by skeletal walls running perpendicular to the plate surface (Pl. 3, fig. 3). There is no specialized attachment area.

The associated tube feet are equally elongate and narrow. They extend only a short distance above the test, becoming taller adradially, where there may be a small sensory tip (text-fig. 3). Septa cross much of the central region leaving a main passageway running around the outer margin of the lumen of the tube foot. In *Dendraster* these septa attach to the skeletal walls that partition the adradial pore. The walls of the tube feet attach to the walls of the conjugate furrow and the margins of the pores. The ampulla is similarly thin-walled and partitioned by septa. Conjugate anisopores are found aborally in many cassiduloids and clypeasteroids.

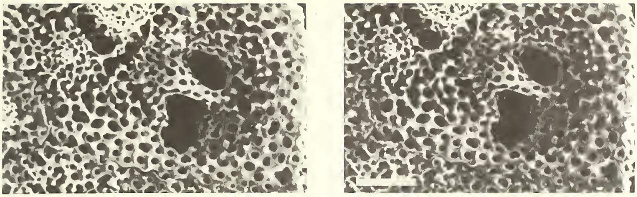
2. *Non-conjugate anisopores* (Pl. 4, fig. 7; text-fig. 14). This category covers all those pore pairs in which one of the pores is markedly different in size or shape from the other and where these pores are not connected with one another by a furrow. In these anisopores there is always a clear periporal area. Such pores are not particularly common and only four examples are reported here. Non-conjugate anisopores are found within the sub-anal fasciole of *M. spatangus* (Lamarck) and *M. nobilis* Verrill. In these it is the perradial pore that is greatly reduced in size so that the neural canal is as large as, if not larger than, the pore itself. The neural canal is axially positioned and an obvious attachment area is developed (text-fig. 14F). The associated tube foot and ampulla were not examined in either species but they are, most probably, much like those of *M. sternalis* and *Brissopsis lyrifera*, described previously.

EXPLANATION OF PLATE 3

Figs. 1–6. *Isopores, anisopores, and unipores*. Top of photomicrograph adapical. 1, stereoview of a partitioned isopore with an axially positioned neural canal from aboral ambulacrum III of *Hemiaster expurgitus* Lovén. 2, *Mellita quinquiesperforata* (Leske). Conjugate anisopores from aboral ambulacrum IV. 3, *Dendraster excentricus* (Eschscholtz). Conjugate anisopore from aboral ambulacrum II. Adradial pores partitioned by calcite septa. 4, *Echinolampas crassa* (Bell). Conjugate anisopore from aboral ambulacrum III. 5, *Apatopygus recens* (Milne-Edwards). Funnelled unipore from the phyllode. 6, stereoview of a funnelled unipore from the phyllode of *E. crassa* Bell.

Scale bar in figs. 5 = 40 μm; 1, 6 = 100 μm; 2–4 = 400 μm.

PLATE 3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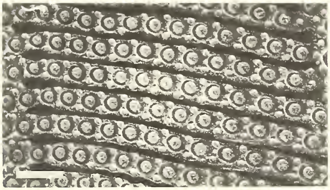
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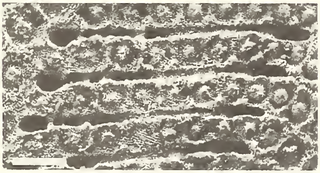
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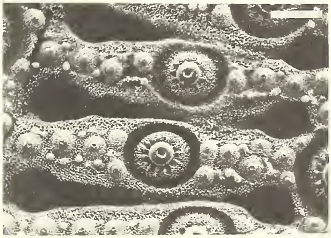
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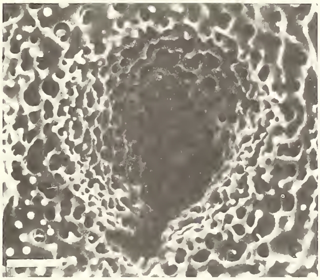
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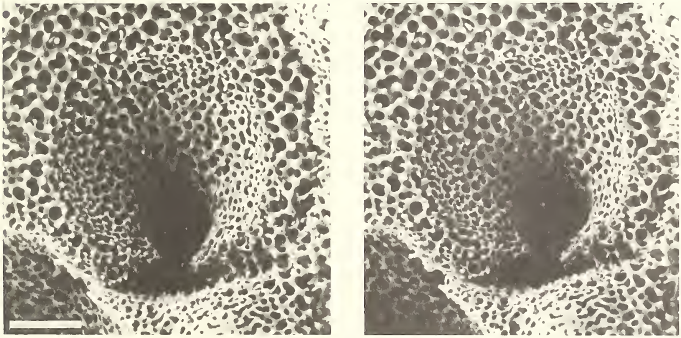
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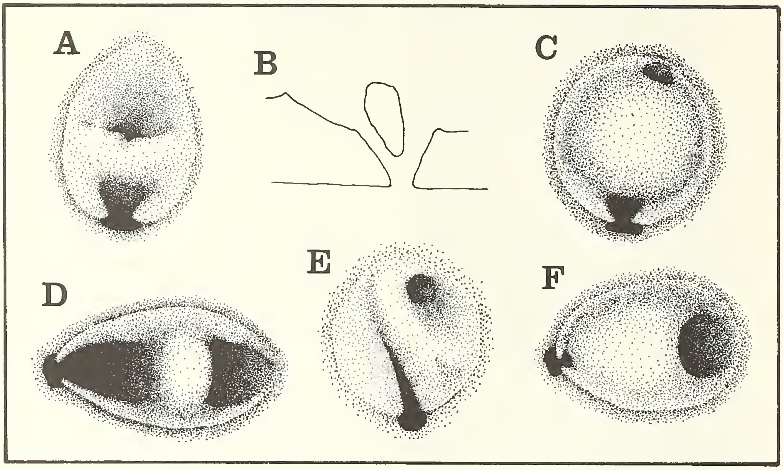
SMITH, Echinoid isopores, anisopores, and unipores



TEXT-FIG. 14. Ambulacral pores observed only at the light microscope level (not to scale). A, phyllode isopore of *Paraster compactus*; B, cross-section of A; C, aboral ambulacrum III isopore of *Faorina chinensis*; D, *Schizaster canaliferus*—aboral ambulacrum III isopore; E, sub-anal anisopore of *Linopneustes murrayi*; F, sub-anal anisopore of *Metalia nobilis*.

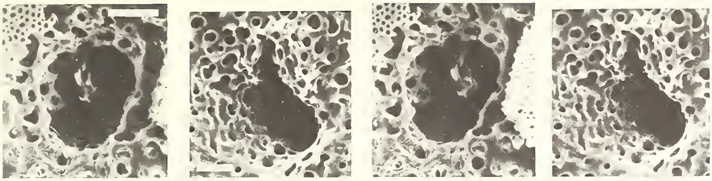
Another type of non-conjugate anisopore is found aborally in ambulacrum III plates of *Maretia planulata*. Here the perradial pore is reduced to a narrow slit, running perpendicular to the adoral plate suture. The adradial pore is circular and lies aboral of the perradial pore (Pl. 4, fig. 7). The neural canal is broad and lies on the major axis of the anisopore. Internally the pores sometimes merge to produce a single pore on the inner plate surface. The anisopore has a flat periporal area around the pores giving it a sub-circular outline. The associated tube foot is cylindrical and terminates in a sensory pad, as in text-fig. 1C. Connective tissue fibres of the tube foot stem insert around the margin of the periporal area. The ampulla is a tubular sack with contractile fibres and no septa. A similar pore structure is found associated with the penicillate sub-anal tube feet of *Linopneustes murrayi* Agassiz (text-fig. 14E). Here, however, the adradial pore appears to lie to one side of the anisopore. There is a broad, circular periporal area but no attachment area rim was seen using a light microscope.

EXPLANATION OF PLATE 4

Figs. 1–7. *Anisopores and unipores*. Top of photomicrograph adapical unless otherwise stated. 1, stereoview of a simple unipore from ambital ambulacrum II of *Echinocardium cordatum* (Pennant). 2, stereoview of a simple unipore from ambital ambulacrum V of *Brissopsis lyrifera* (Forbes). Small periporal area to the adapical edge. 3, stereoview of two oral micro-unipores from *Encope michelini* Agassiz. Right side of photomicrograph adoral. 4, stereoview of an oral micro-unipore from *Mellita quinquiesperforata* (Leske). 5, stereoview of an oral micro-unipore from *Clypeaster rosaceus* (Linnaeus). 6, stereoview of two oral micro-unipores of *Dendraster excentricus* (Eschscholtz) from the floor of a food groove. 7, stereoview of a non-conjugate anisopore from aboral ambulacrum III of *Maretia planulata* (Lamarck).

Scale bar in figs. 4 = 10 μm; 3, 5 = 20 μm; 1, 2, 6 = 40 μm; 7 = 100 μm.

PLATE 4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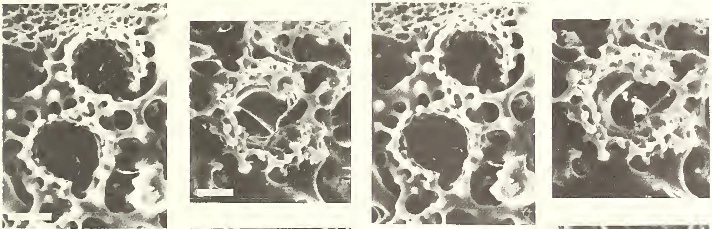
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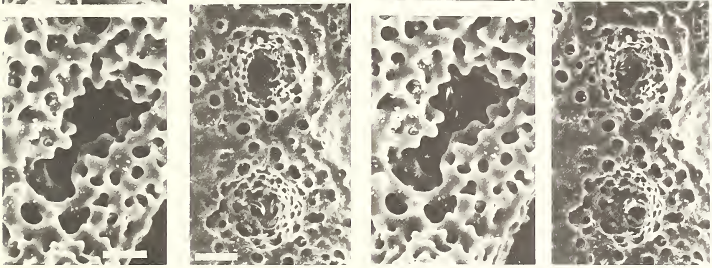
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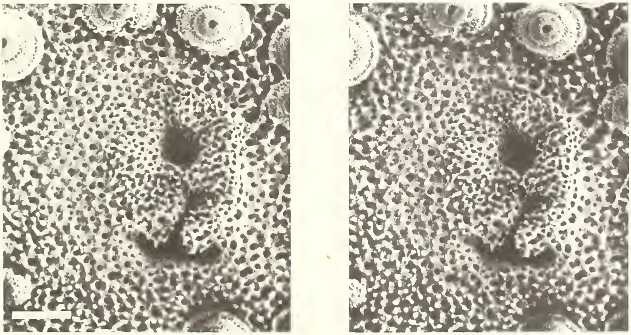
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SMITH, Echinoid anisopores and unipores

Unipores

There is a great deal of variation in the structure of unipores in irregular echinoids and there is a corresponding variation in the morphology of the associated tube foot. Unipores can be grouped according to the pore size, the presence or absence of an attachment area, and the extent of the periporal area.

1. *Simple unipores* (Pl. 4, figs. 1, 2). These are small pores, 50 μm to 100 μm in diameter, roughly circular in outline. There is no periporal area and no rim of specialized stereom forming an attachment area. The neural canal is large yet poorly differentiated with only a small ridge on either side of the pore to distinguish it. Simple unipores are found ambitally in the lateral and posterior ambulacra of many spatangoids. In *E. cordatum* much of the pore space is taken up with nervous tissue and the tube foot is reduced to a sensory hummock capable of little extension (text-fig. 1ii). No ampulla is found in association.

2. *Micro-unipores* (Pl. 4, figs. 3–6; text-fig. 8). These are small pores, usually 20 μm to 50 μm in diameter though very occasionally up to 80 μm in diameter. They are surrounded by an attachment area of fine stereom which typically forms a rim to the pore. In most, there is a clearly defined neural canal though this may be absent from some of the larger pores.

Micro-unipores are found only in clypeasteroids where they are associated with minute tube feet which end in a functional sucking disc (text-fig. 8). The smaller micro-unipores, with a distinct neural canal, bear slender and highly active tube feet. The larger micro-unipores, which are only found in or adjacent to food grooves, have much shorter tube feet with relatively broader discs. All ampullae are cylindrical and lack septa.

3. *Funnelled unipores* (Pl. 3, figs. 5, 6; Pl. 5, figs. 1, 2; text-fig. 7). In these unipores there is a narrow attachment area which forms a horse-shoe-shaped rim, 100 μm to 500 μm in diameter. The area inside this rim slopes inwards fairly steeply to a single pore. There is a neural canal on the adoral side of this pore. The unipore may be circular or oval in outline. In larger pores, near the peristome, the unipore rim may be partially surrounded by a depressed region of the plate surface which accommodates a tract of sub-epidermal nervous tissue.

Funnelled unipores are found in association with oral and ambital tube feet of cassiduloids and with buccal tube feet of clypeasteroids. In the cassiduloids all such tube feet have a functional sucking disc (text-fig. 7) but buccal tube feet of clypeasteroids may not be suckered. In either case, ampullae are cylindrical and lack septa.

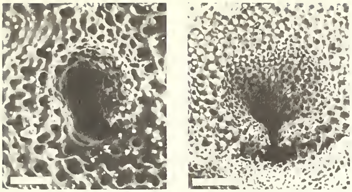
4. *Unipores with an extensive periporal area* (Pl. 2, fig. 4; Pl. 5, fig. 7; Pl. 6, figs. 1–3; text-fig. 9). These are very large and very distinctive unipores with a diameter of between 500 μm and 2 mm. There is a relatively small pore, with a clear neural canal, situated on the adoral or perradial margin of the unipore. The rest of the unipore is formed from a very extensive periporal area which commonly forms a platform but which may be developed into a bulbous dome centrally (Pl. 6, fig. 3). Surrounding the periporal area is a narrow attachment area, either forming a marginal rim or forming the outer slope to the periporal platform.

EXPLANATION OF PLATE 5

Figs. 1–7. *Unipores.* Top of photomicrograph adapical unless otherwise stated. 1, stereoview of a funnelled unipore of *Apatopygus recens* (Milne-Edwards) from ambital ambulacrum II. 2, stereoview of a funnelled unipore of *Echinolampas crassa* (Bell) from ambital ambulacrum III. 3, stereoview of a broad-rimmed unipore of *Brissus latecarinatus* (Leske) from aboral ambulacrum III. 4, stereoview of a broad-rimmed unipore of *Paramaretia peloria* (Clark) from aboral ambulacrum III. 5, stereoview of a broad-rimmed unipore of *Echinocardium pennatifidum* Norman from aboral ambulacrum III. 6, stereoview of a sub-anal unipore rimmed by an attachment area of *E. cordatum* (Pennant). Left side of photomicrograph adoral. 7, stereoview of a phyllode unipore with an extensive periporal area from *Brissopsis lyrifera* (Forbes).

Scale bar in figs. 1 = 40 μm; 2–5 = 100 μm; 6, 7 = 200 μm.

PLATE 5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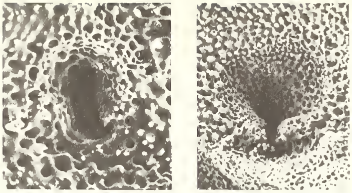
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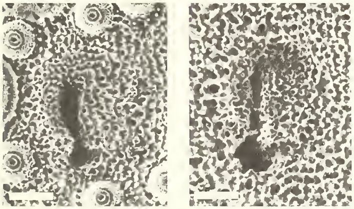
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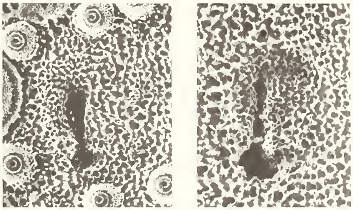
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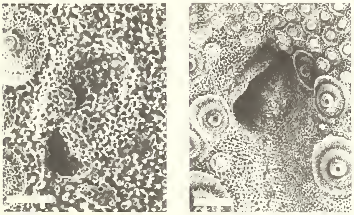
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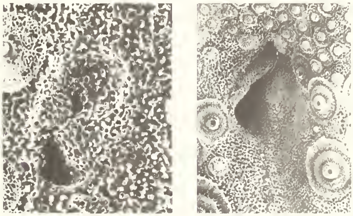
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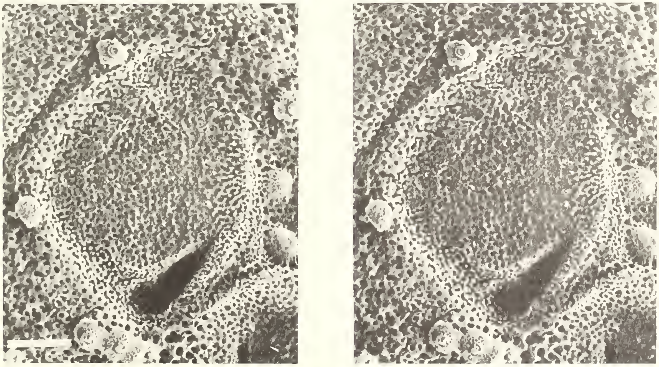
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SMITH, Echinoid unipores

This type of unipore is found with penicillate tube feet of the phyllode in nearly all species of spatangoid examined as well as in the holasteroids *Plexechinus nordenskjoldi* Mortensen and *U. naresianus* Agassiz. In addition, the dorsal, funnel-building tube feet in four species of *Brissopsis* (*B. lyrifera* (Forbes), *B. luzonica* Gray, *B. alta* Mortensen, and *B. atlantica* Mortensen) are found with this type of unipore (Pl. 6, figs. 1, 3, and Chesher 1968, pl. 6, fig. f). Some funnel-building tube feet of the sub-anal fasciole are also associated with this type of unipore in *B. lyrifera*, *B. luzonica*, and *Agassizia scrobiculata* Agassiz and Desor. It therefore appears that unipores with an extensive periporal area bear penicillate tube feet and have tubular ampullae lacking septa.

5. *Constricted unipores* (text-fig. 10). Constricted unipores are obviously incomplete isopores where, either growth of the interporal partition has ceased before the two ridges, which go to form the partition, have met and fused, or where later resorption has removed the central part of the interporal partition. This central constriction gives the pore a very distinctive appearance. An axially positioned neural canal is present and there is a fairly obvious rim to the margin which, no doubt, marks the attachment area.

Constricted unipores tend to be found along with isopores. In *U. wyvillei* (Agassiz) many of the penicillate tube feet of the phyllode are associated with constricted unipores. Sub-anal pores of *Protenaster australis* (Gray), *Schizaster canaliferus* (Lamarck), and *Diploporaster savignyi* (Fourtau) may be isopores or may be constricted unipores. The associated sub-anal tube feet have not been examined but it seems likely that they have a disc of papillae, as in other species. Kier (1974) records similar pores in a number of other spatangoids.

6. *Unipores rimmed by a periporal area* (Pl. 2, fig. 6; Pl. 5, figs. 3–5; text-fig. 1III). In these, the pore is typically rather elongate and narrow and the neural canal, which lies at the adoral end of the pore, is often elongate in a direction roughly perpendicular to that of the pore. These unipores vary in size from about 100 μm up to 400 μm in length. In small unipores, generally less than 200 μm in length, the neural canal is relatively large and the periporal rim narrow and U-shaped. In larger unipores the periporal area becomes relatively broad and is circular or ovoid in outline. The pore in these broad-rimmed types forms only a small, central part of the unipore (Pl. 5, figs. 3, 4). The periporal rim is planar. Connective tissue fibres of the stem of the tube foot insert around the margin of the unipore but the stereom construction is not always modified to produce a distinct attachment area.

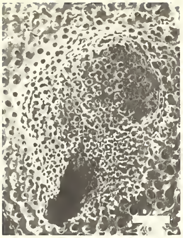
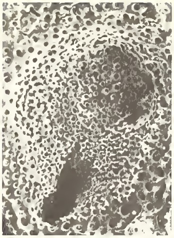
Small, rimmed unipores are developed ambitally in many spatangoids where they are associated with small, cylindrical tube feet which terminate in a sensory pad. Similar pores are found aborally in all ambulacra of the holasteroids *U. naresianus* Agassiz and *U. wyvillei* (Agassiz). The larger broad-rimmed unipores are found aborally in ambulacrum III of a number of spatangoids and adapically in ambulacrum III of the holasteroid *Pourtalesia miranda* Agassiz. These bear large sensory tube feet which are again suckerless. Only in *E. pennatifidum* were broad-rimmed unipores found bearing penicillate, funnel-building tube feet (text-fig. 11III; Pl. 5, fig. 5).

EXPLANATION OF PLATE 6

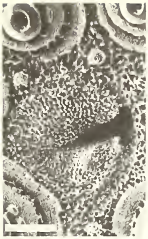
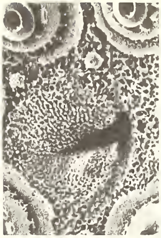
Figs. 1–5. *Unipores and isopores.* 1, stereoview of a unipore with an extensive periporal area in aboral ambulacrum III of *Brissopsis lyrifera* (Forbes). Left side of photomicrograph adoral. 2, stereoview of a sub-anal unipore with an extensive periporal area from *B. lyrifera* (Forbes). Top of photomicrograph adapical. 3, stereoview of a unipore with an extensive periporal area in aboral ambulacrum III of *B. atlantica* Mortensen. Left side of photomicrograph adoral. 4, stereoview of unipores rimmed by an attachment area in aboral ambulacrum III of *Echinocardium cordatum* (Pennant) showing the difference in shape of perradial and adradial unipores. Left side of photomicrograph adoral, perradius to bottom. 5, stereoview of two aboral petal isopores seen on the inner plate surface of ambulacrum V in *E. cordatum* (Pennant).

Scale bar in figs. 1, 3 = 100 μm; 2, 4 = 200 μm; 5 = 400 μm.

PLATE 6

1

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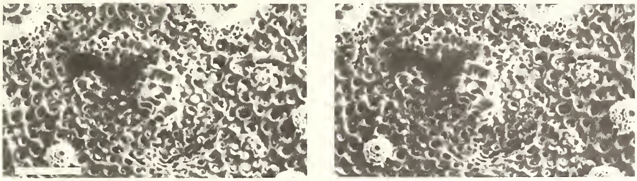

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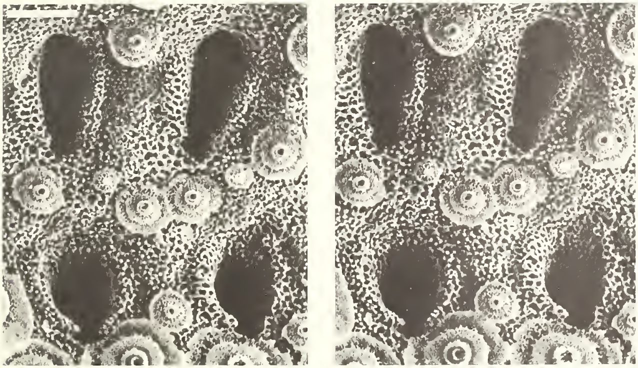
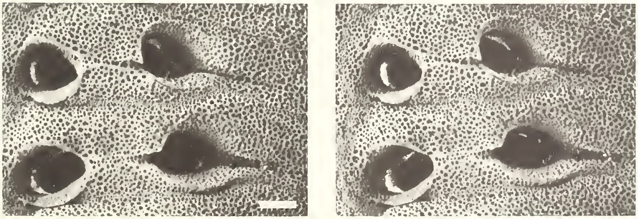


4



5

SMITH, Echinoid unipores and isopores

7. *Unipores rimmed by an attachment area* (Pl. 5, fig. 6; Pl. 6, fig. 4; text-figs. 10, 11iv). These are large unipores, between 300 μm and 800 μm in diameter, which are circular to ovoid in outline. There is no periporal area but a narrow rim of attachment area borders the pore. A neural canal is present in a perradial position. Adradially the attachment area becomes less clearly defined. These unipores are, in some respects, similar to funnelled unipores but have more or less vertical pore walls. They can be distinguished from unipores rimmed by a periporal area by the size and shape of the pore, which, in this case, forms a very large part of the unipore.

Unipores rimmed by an attachment area are found in aboral ambulacrum III of *E. cordatum* where they bear penicillate, funnel-building tube feet (text-fig. 11iv). They are also found within the sub-anal fasciole in *E. cordatum* and *Spatangus raschi* where they again are associated with penicillate, funnel-building tube feet. The accompanying ampullae are bulbous tubes, lacking septa and with a well-developed layer of contractile fibres.

FUNCTIONAL SIGNIFICANCE OF THE STRUCTURE OF TUBE FEET

Respiratory tube feet. All specialized respiratory tube feet are connected to a large and flattened ampulla by two pores. This permits a one-way flow of coelomic fluid through the tube foot/ampulla system with one pore carrying fluid into the tube foot while the other carries fluid out of the tube foot (see Fenner 1973 for details). The aboral tube feet of most irregular echinoids are modified for gaseous exchange in a number of ways.

1. The tube feet and ampullae are very thin-walled possessing only a single layer of epithelial cells on either side of a very thin layer of connective tissue fibres, which generally is only 1 μm to 5 μm in breadth. Muscle fibres, although present, are sparsely distributed. Both connective tissue and muscle act as a barrier against the diffusion of gases, and therefore tube feet specialized for gaseous exchange are much thinner-walled than other tube feet.

2. Elongation of the tube foot not only increases the total surface across which gaseous exchange can occur but also increases the surface area to volume ratio making a more efficient system for gaseous exchange.

3. The development of a central, partitioned region in specialized respiratory tube feet serves two main functions. First, the septa, which connect the opposing walls, ensure that the tube foot maintains its narrow, elongate shape during expansion and contraction. Secondly, these septa separate the inflowing coelomic fluid into many streams ensuring that full use is made of the entire central region of the tube foot. This central region not only increases the surface area of the tube foot but also isolates the inflowing, oxygen-poor current from the outflowing, oxygen-rich current. In unspecialized tube feet these two currents are separated simply by a thin septum and depletion of oxygen from the outflowing oxygenated fluid can occur across the septum.

4. Lateral extension of the tube foot is accompanied by a reduction in its height. This is a direct result of the infaunal mode of life led by irregular echinoids. In regular echinoids, such as *Arbacia*, respiratory tube feet are able to extend well beyond the spines so as to obtain a suitably large surface area. These tube feet are relatively tall and narrow. With the development of an infaunal mode of life in the irregular echinoids, respiratory tube feet have to be protected from abrasion by sediment particles and can therefore extend no further than the tips of the adjacent, protective spines. These spines can be very short, especially in sand dollars. Therefore, in order to maintain a large surface area for efficient gaseous exchange, the tube feet have to become very elongate.

5. The more elongate tube feet are typically skewed so as to be tallest above the adradial pore. This is the pore through which coelomic fluid passes into the tube foot and there is a major vertical passageway in the lumen of the tube foot directly above this pore. Presumably, by having this vertical passageway as the tallest part of the tube foot, the inflowing current is better distributed through all the pathways in the central, partitioned region.

6. The development of side-branches to the central, partitioned region of the tube foot increases the surface area for gaseous exchange without adding to the height of the tube foot.

There appears to be some correlation between the development of specialized respiratory tube feet and the size and habitat of the urchin. Small echinoids, such as *Apatopygus*, *Cassidulus*, *Echinocyamus*, *Hemiaster*, and *Palaeostoma* have less specialized tube feet than larger urchins such as *Echinolampas*, *Mellita*, *Spatangus*, and *Echinocardium*. This is likely to be the result of differences in the surface area to volume ratio of the urchins. Some deep-sea urchins have not developed specialized respiratory tube feet. *Urechinus* and *Pourtalesia* have only small, sensory tube feet, borne on unipores, in their aboral ambulacra. Another deep-sea echinoid, *Goniospatangus*, also appears to lack specialized respiratory tube feet, judging from its partitioned isopores. Only the pygasteroids and holectypoids have never developed respiratory tube feet aborally.

Funnel-building tube feet. The terminal disc of dorsal and sub-anal tube feet is often highly modified in comparison with the suckered tube feet of regular echinoids. Funnel-building tube feet differ from suckered tube feet in the following points.

1. The disc relies on mucus rather than suction for its adhesiveness although, in many cases, levator muscles are still present to control the shape of the disc. This enables the tube foot to transport a disc-full of small particles, which would be impossible using a sucking disc. Although some spatangoids live in shell gravels and have to cope with individual grains, most excavate in sands or muds where the particle size is much smaller than the size of the disc.
2. The surface area of the disc is increased. In the simpler forms of funnel-building tube feet the disc is broad and is largely covered by an epithelial pad with mucous glands. The surface area of mucous-producing epithelium is greatly increased by the development of papillae in more specialized tube feet.
3. The disc becomes more flexible. In regular echinoids, the rosette is usually made up of four or five elements firmly sutured together to produce a fairly rigid disc. In funnel-building tube feet of spatangoids, the rosette, where present, is composed of between eight and fifty radially arranged rods. The rods are bound together by connective tissue over much of their length in the least specialized tube feet, though distally they become independent from one another. In others, the rods are elongate and are bound together only at their proximal end. The increase in the number of elements which form the rosette presumably gives more flexibility to the disc since muscle fibres can now act on relatively small segments of the disc. Flexibility is increased by the indentation of the margin between rods, which produces a rim of finger-like papillae. The most flexible disc occurs where the rods have separated from one another proximally so that each papilla is independent of its neighbours. Where the papillae are numerous and form more than one row, muscle control on individual rods is reduced, since muscle fibres are arranged to act radially on the disc margin.
4. In penicillate tube feet the lumen extends into the disc. This coincides with the development of independent rods. With the loss of a cohesive rosette it becomes impossible to support a broad terminal disc and papillae would have to be arranged on a simple rounded tip. However, by extending the lumen laterally it is possible to support a broad disc by hydrostatic pressure. In order to maintain the shape of the disc during expansion and contraction of the tube foot, radially arranged septa cross the lumen of the disc, binding the upper and lower surfaces together. The extension of the lumen is therefore vital to the formation of a broad, penicillate disc. The presence of the lumen in the disc has another effect, in that the shape of the disc, although stabilized by septa, is apparently more flexible than in discs with rosettes. This makes the disc much more prehensile.

The development of penicillate tube feet appears to have resulted from a need to pick up and transfer sediment particles. Whereas all sub-anal and phyllode tube feet of spatangoids that were examined are penicillate, very few dorsal, funnel-building tube feet are known to be penicillate. In *E. pennatifidum* and *Breynia australasia* there is a ring composed of a few large papillae around the margin of the disc of dorsal, funnel-building tube feet. In *E. cordatum* and *Agassizia scrobiculata* these tube feet have discs with numerous papillae. All other species known have a rosette of rods in dorsal funnel-building tube feet.

Phyllode tube feet have to pick up particles and transfer them into the mouth. Sub-anal tube feet have also been reported to transfer sediment particles. These tube feet build either one or two horizontal tubes posterior to the animal. In *Brissopsis alta* (Chesher 1968) and *E. cordatum* (Nichols 1959*a*, *b*), sub-anal tube feet collect particles from the end of the tube and carry them back to the vicinity of the sub-anal tuft of spines where they are dropped and incorporated into the walls of the funnel. The extension of the lumen into the disc and the flexibility of the papillae are extremely important since they allow the disc to change shape, as observed by Nichols (1959*a*, *b*) and Chesher (1968). During protraction the disc is convex and the papillae splayed, but upon contact with a suitable area of sediment the disc flattens. Upon contraction the disc invaginates and the papillae converge to envelop the adhering sediment particles. When phyllode tube feet reach their destination the disc is everted to drop its load. The situation is probably similar in sub-anal tube feet.

In building a vertical respiratory shaft to the surface, the problem of transporting particles is much less critical. Chesher (1968) observed that dorsal, funnel-building tube feet of *B. alta* were pressed into the substrate, oscillated, and then removed, leaving a circular indentation. He was unable to ascertain whether sediment was compressed or whether it was removed by the tube feet. It may be that the uppermost few centimetres of sediment are less compact and that a funnel can be built by simply compressing the sediment. However, it seems more probable that the tube feet do pick up some particles and that those which do not adhere or that are knocked off, fall down the funnel into the chamber of the burrow. Thus adhesion and transportation of sediment particles is not particularly important since those particles that are loosened by the action of the tube feet are automatically lost from the funnel. In this respect it is interesting to note that *E. cordatum*, one of the two known spatangoids with well-developed penicillate tube feet in ambulacrum III, can extend these tube feet out of the respiratory funnel where they gather detritus from the surface layer of sediment and carry this down into the burrow (Robertson 1871; Buchanan 1966). *A. scrobiculata* may also feed in this way.

In a number of spatangoids the aboral tube feet in ambulacrum III are suckerless. Aboral sensory tube feet are present in species of *Brissus*, *Lovenia*, *Maretia*, *Meoma*, *Paramaretia*, and *Spatangus*. Most of these are known to live infaunally (Takahashi 1938; Tornquist 1911; Ferber and Lawrence 1976; Chesher 1969; Nichols 1959*b*) but they rarely maintain any connection with the surface and then only by means of their dorsal spines. These echinoids are therefore restricted to living in sands or gravels where interstitial water circulation can be promoted. The dorsal tube feet of ambulacrum III are used simply as sense organs.

Oral tube feet. Irregular echinoids feed mostly by ingesting large quantities of sediment. The tube feet that are involved in collecting and transporting sediment particles are suckered in the holectypoids, cassiduloids, and clypeasteroids but are penicillate in the holasteroids and spatangoids. This seems to be related to the grain size of the substrate ingested. Recent cassiduloids and holectypoids live in coarse sands and shell gravels which they ingest with only limited selectivity (Higgins 1974; Thum and Allen 1976; Gladfelter 1978; Rose 1978). Suckered tube feet are quite satisfactory for picking up and transporting individual grains which are equal to or larger in size than the disc. Other groups have, however, invaded finer-grained substrates. The problem of feeding in these finer substrates has been solved in three ways:

1. In clypeasteroids, which live largely on or within sands, the tube feet have become extremely small but have retained a functional sucking disc. They have also become exceedingly numerous. These minute tube feet have a small enough sucking disc to be able to pick up the small sand and detritus particles which surround them. These can then be transferred to a near-by mucous rope, which lies in each food groove, or directly to the mouth.
2. In spatangoids and some holasteroids, large penicillate tube feet are developed around the peristome. Each tube foot can pick up a disc-full of fine sediment particles by mucous adhesion. These prehensile tube feet are even retained in spatangoids that live in coarse sands and shell gravels.
3. In *Pourtalesia* only sensory tube feet occur around the mouth. Unlike other irregular echinoids the anterior ambulacrum is deeply invaginated below the ambitus and the walls and roof of this cavity are covered in highly modified spatulate spines. This echinoid probably ploughs through the

surface layer of sediment using its specialized spines to shovel material into the peristome. This explains why *Pourtalesia* leaves behind a shallow furrow as it moves forward. This is illustrated in Southward *et al.* (1976) and has also been observed in bottom photographs by D. S. M. Billett (pers. comm.).

Ampullae. There are only two types of ampulla in irregular echinoids. Firstly there are those which are very large and elongate and which are crossed by numerous septa. These septa maintain the shape of the ampulla during contraction and expansion and also help to partition the flow of coelomic fluid so as to make full use of the large surface area available. Although there are contractile fibres in the walls, these ampullae are primarily designed for gaseous exchange. They are always connected to their tube foot by two pores. The corrugated ampullae in *E. cordatum* are associated with a conjugate furrow on the inner plate surface (Pl. 6, fig. 5; text-fig. 5).

Secondly there are cylindrical or bulbous ampullae which connect with the branch of the radial water vessel by a relatively narrow neck. These ampullae have no septa crossing the lumen and have a well-developed layer of circular, interconnecting contractile fibres. These accompany non-divergent isopores and unipores and serve as reservoirs for the tube foot. Thus they permit rapid expansion and contraction of the tube foot, independent of the contraction or expansion of neighbouring tube feet.

Intermediates do occur, as, for example, in *Echinoneus cyclostomus*, where the ampulla is squat and crossed by relatively few septa (text-fig. 6).

FUNCTIONAL SIGNIFICANCE OF THE STRUCTURE OF PORES

Number of pores. Two pores connecting the tube foot with its ampulla allow a one-way flow of coelomic fluid, as observed by Fenner (1973). This is highly adaptive, since the continuous circulation that results enhances the efficiency of gaseous exchange across the test. Where known, fluid passes into the tube foot via the adradial pore and out of the tube foot via the perradial pore.

In unipores, fluid moves in and out of the tube foot only during expansion and contraction (Fenner 1973). Kier (1974) has noted an evolutionary trend in irregular echinoids for oral pores to change from double to single pores. Unipores come to replace pore pairs where the associated tube foot plays only a minor part in supplying the respiratory demands of the animal. This usually follows the development of specialized, aboral, respiratory tube feet.

Pore divergence. Not all isopores and anisopores bear tube feet that play an important role in gaseous exchange. The emphasis placed on gaseous exchange is reflected in the separation of the two pores. If the pores are well separated when they appear on the inner surface of the test, then the associated ampulla is large and flattened and is crossed by many septa. If the pores coalesce, or appear close together on the inner plate surface, then the associated ampulla is cylindrical or bulbous and is not crossed by septa. Therefore tube feet associated with divergent pores, or pores that are widely separated on the outer surface of the plate, have a primary or secondary respiratory function. Tube feet associated with closely spaced pores, which show little or no divergence and which may even coalesce internally, play no significant part in gaseous exchange across the test. It is often the case that areas of non-divergent isopores may include some constricted unipores.

Overall shape. Isopores that are circular or oval in outline bear tube feet which have a cylindrical stem and terminate either in a sensory pad or in a disc. Isopores that are obviously elongate bear specialized respiratory tube feet with a central, partitioned region. The same is also true of anisopores. The shape of the ambulacral pore obviously matches the shape of the base of the tube foot.

Most unipores are roughly circular in outline. Where they are dense and become arranged into more than just a single row, differences in shape are found. This occurs aborally in ambulacrum III of *Echinocardium cordatum* (Pl. 6, fig. 4) and in the phyllodes of certain cassiduloids, such as

Apatopygus recens. The pores that lie nearest the perradial suture are typically circular in outline, whilst those in an adradial position are more elongate. This does not signify a difference in the structure or function of the associated tube feet but appears to result from the angle at which the pore passes through the plate. Elongate unipores occur with the more oblique pores.

Size. The size of ambulacral pores is of little importance in interpreting the form of the associated tube foot. For example, in this survey the tube feet which were found to terminate in a sucking or adhesive disc are associated with unipores that range from 20 μm to 2000 μm in diameter, whereas sensory tube feet are associated with unipores that range from 50 μm to 500 μm in diameter. Pore size does, however, indicate the size of the associated tube foot and this can be useful when comparing the same type of ambulacral pore in different species.

Pore shape. In isopores, elongate pores are always associated with respiratory tube feet. Pores, that are approximately circular in outline, are found with sensory, suckered, adhesive, or respiratory tube feet. In conjugate anisopores the adradial pore is always very elongate. As this pore passes through to the interior of the test it narrows considerably (text-fig. 13E). This is the pore through which coelomic fluid flows into the tube foot and the reason for its great elongation lies in the fact that the associated tube foot, although very elongate, rises only a short distance above the level of the test. This, as was explained previously, is an adaptation found in infaunal echinoids to provide efficient, but protected, respiratory tube feet. Were the septa to be arranged parallel to the plate surface, as in tall respiratory tube feet, little separation of the outflowing current could take place. In order to avoid this the septa are arranged obliquely and the adradial pore is elongate. In this way the outflowing coelomic fluid can be separated efficiently and much better use made of the central partitioned region. Because the tube foot is so short, partitioning often starts within the pore before it reaches the plate surface. This may be done by extension of the septa into the pore or by the growth of calcite partitions within the pore, as in *Dendraster*.

In unipores, large, round pores are associated with active tube feet that terminate in some form of disc. Small, narrow, and elongate pores are usually associated with sensory tube feet though occasionally unipores with an extensive periporal area, that are associated with feeding or funnel-building tube feet, may have a slit-like pore. In spatangoids, where the pore is large and forms a large percentage of the area of the unipore, as in the aboral unipores of ambulacrum III in *E. cordatum*, the associated tube feet are highly extensible. These tube feet, in *E. cordatum* can build a tube up to 18 cm in length (Nichols 1959*b*). Unipores, where the pore forms only a small proportion of the unipore, support tube feet which are less extensible. These are commonly sensory tube feet but in species of *Brissopsis* and in *E. pennatifidum* funnel-building tube feet are associated with these unipores. It is interesting that none of these appear to be capable of building a respiratory funnel more than 2 to 3 cm in length (Chesher 1968; Buchanan, in Goldring and Stephenson 1970; Gage 1966). Unipores associated with phyllode tube feet also have a relatively small pore and again appear to be only moderately extensible. The large area of pore is presumably required for the efficient movement of large volumes of coelomic fluid in and out of the tube foot.

Funnelled unipores are so shaped because of the construction and growth of the plate. In Recent cassiduloids there is a thick outer plate layer. The pore funnels outwards as it passes through this layer, presumably due to the expansion of the tube foot during growth of the outer plate layer. In fossil cassiduloids, such as *Clypeus* and *Galeropygus*, this outer plate layer is not developed and ambulacral pores, although partitioned, are not funnelled and are rimmed by an attachment area (Pl. 2, fig. 6).

Neural canal. The neural canal houses a branch of the radial nerve, part of which extends up the tube foot and part of which merges with the sub-epidermal nerve plexus of the plate surface. A neural canal is absent, or only feebly developed, in pores associated with respiratory tube feet, since very little nervous tissue passes up the perradial pore. A neural canal is present in pores supporting other tube feet. The neural canal is nearly always separated from the perradial pore by a constriction.

A thin membrane of connective tissue stretches across here, separating the nervous tissue from the lumen of the pore. The pore, in simple unipores, is analogous to a neural canal, since it is taken up largely by nervous tissue. In this case the narrow lumen of the water vascular system is not usually separated from the nervous tract by a constriction. It is similar, in this respect, to the terminal tube foot of the ocular plates.

In some instances the neural canal may become separated from the perradial pore by the closure of the constriction to form an unbroken attachment area, or becomes separated on its passage through to the interior of the test. Both are relatively rare occurrences and the formation of an independent neural pore is an abnormal situation of little functional significance.

Whether the neural canal lies on, or is displaced from, the major axis, is an important feature of partitioned isopores. This is linked with the presence or absence of pore divergence. General-purpose tube feet, involved in gaseous exchange across the test as well as in sensory reception and/or adhesion, have flattened and elongate ampullae. In order to attain a suitably elongate ampulla, the two pores must diverge as they pass through the test. In order to optimize this divergence, the major axis of the isopore is aligned parallel with the branch of the radial water vessel serving it. This is the direction in which the ampulla is flattened. The neural canal always maintains contact with the adoral plate suture and therefore lies to one side of the axis of the isopore.

With the development of specialized respiratory tube feet, other tube feet do not have to assist in gaseous exchange across the test. The ampullae therefore become cylindrical or bulbous tubes with narrow necks. No pore divergence is necessary and, rather than having a pore for inflowing coelomic fluid positioned perradially and one for outflowing coelomic fluid positioned adradially, both pores come to lie side by side, more or less equidistant from the radial water vessel. This is brought about by a shift of the adradial pore to an aboral position relative to the perradial pore. The neural canal remains in an adoral position, in contact with the adoral plate suture and thus comes to lie in an axial position.

This trend is evident in the partitioned isopores of regular echinoids. In the isopores that accompany the most muscular tube feet (P4-type), the adradial pore is shifted so that the major axis of the pore lies oblique to the adoral plate suture. The neural canal therefore comes to lie almost in an axial position. The pore divergence that occurs in these isopores is less than in most other types of partitioned isopore found in regular echinoids and the associated ampulla is also smaller and squatter.

The adapical/adoral isopore orientation is presumably the primitive condition and is still found in many spatangoids. However, with the development of more numerous tube feet aborally in ambulacrum III, the adradial pore shifts back to an adradial position to permit closer packing of the tube feet. The two pores still run parallel to one another and the axial position of the neural canal has been maintained. The attachment in such isopores is well developed adapically and adorally but is feebly developed adradially and is interrupted by the neural canal perradially. The axial-positioning of the neural canal is therefore not fortuitous but is brought about by the fact that funnel-building tube feet of ambulacrum III have to work largely in one plane.

Attachment area. Compared with most ambulacral pores of regular echinoids, the attachment area is poorly developed in the ambulacral pores of irregular echinoids. This is because the tube feet of irregular echinoids, with the possible exception of *Echinoneus cyclostomus*, are never involved in anchorage and require little tensile strength. Stem muscle fibres are therefore poorly developed and form only a thin layer, rarely more than a few fibres thick and often less. These muscle fibres simply control the posture of the tube foot. The development of the attachment area is not as useful in determining the structure of the overlying tube foot in irregular echinoids as it is in regular echinoids. It is important, however, that the attachment area, an area of fine labyrinthic stereom, be distinguished from the periporal area, an area of coarser and denser stereom overlain by squamous epithelium.

Even in partitioned isopores the development of the attachment area does not give much information. In most there is a clear but narrow attachment area. This may, however, be very indistinct in small pores (Pl. 3, fig. 1), and it may be difficult to correctly identify suckerless tube feet from the structure of the pore.

Periporal area. A large periporal area is developed in certain unipores. It lies within the base of the tube foot and is covered by a single layer of squamous epithelium. It may be developed for one of two reasons. First the pore may be reduced in size, often to a slit-like opening, where extensive expansion and contraction of the tube foot with the associated shifting of coelomic fluid is not important. This is common in sensory tube feet where the associated unipore has a small central pore surrounded by a horse-shoe-shaped periporal area. Secondly the associated tube foot may terminate in a very broad disc. The stem required to support it has to have a large diameter so that the pore, although not small, forms only a small part of the unipore. The pore has a marginal position and the periporal area may be depressed, flush, or raised and is sometimes developed into a broad, bulbous dome. There is no obvious functional significance underlying this variation though a central dome may help to maintain coelomic fluid movement in the lumen by increasing the surface area of rather sparsely ciliated epithelium.

Interporal partition. The interporal partition may be crossed by a furrow, a narrow platform, or by a band of distinctive stereom linking the two pores together. In all cases the associated tube foot is specialized for gaseous exchange. The narrow zone that crosses the interporal partition marks the position of the central, partitioned region of the tube foot. The more complex and branched tube feet have isopores in which the connecting band of distinctive stereom is displaced adapically in an arc. This may be in response to the lop-sided development of lobes in the central, partitioned region, noted by Fenner (1973) in spatangoid respiratory tube feet.

In partitioned isopores and anisopores the interporal partition is commonly raised above the level of the plate surface, but may also be flush or sunken. A septum joins on to the interporal partition in partitioned isopores with a laterally positioned neural canal, as in *Echinoneus*, but is absent from tube feet associated with partitioned isopores with an axially positioned neural canal. In some pore pairs the pores coalesce internally so as to produce an interporal partition that bridges the pore on the outer surface (text-fig. 14A, B; Kier 1974, fig. 24B). In constricted unipores the partition has obviously been breached or left incomplete. Kier (1974) has shown that, during evolution, the interporal partition is lost from oral pore pairs of irregular echinoids. Thus with the loss of its role in gaseous exchange, a tube foot loses its septum and the interporal partition becomes redundant and may be lost at a later stage.

The identification of funnel-building tube feet in fossil echinoids. From the preceding descriptions it must, by now, be apparent that funnel-building tube feet of spatangoids can be associated with several different kinds of pores. The ability to identify these tube feet in fossils would be extremely useful to the palaeoecologist and has prompted three workers to suggest features distinctive of the associated pores. Nichols (1959*b*) used the presence of a large interporal bulge and a surrounding non-tuberculated area to indicate that the associated tube feet were muscular and terminated in some form of disc. Kier (1974) also noted that a deep adapical pit was often found in the peripodia which bore funnel-building tube feet and suggested that this also might act for muscle attachment. We now know, however, that funnel-building tube feet need not be particularly muscular and that the interporal bulge and adapical depression have nothing to do with muscle attachment. Bromley and Asgaard (1975) suggest that spatangoids capable of forming an apical funnel of any great length require more than fifty aboral tube feet and an associated fasciole. No reason is given why so many tube feet are required dorsally when six to ten sub-anal tube feet suffice, in many cases, for building an extensive sub-anal funnel.

Although the results of this work show that it is not possible to reconstruct the form of the terminal disc from the pore morphology it is usually possible to distinguish between those pores that bear sensory tube feet and those that bear funnel-building tube feet. The following features are important when trying to reconstruct the tube feet in fossil spatangoids.

1. The presence or absence of an appropriate fasciole cannot be used to infer the presence or absence of funnel-building tube feet. Although Recent spatangoids, which lack an aboral fasciole, possess only sensory tube feet in the aboral part of ambulacrum III, this is unlikely to hold true for the more primitive fossil spatangoids, such as *Micraster*. In *Micraster* the whole of the aboral surface is covered in miliaries interspersed with tubercles (a situation not encountered in Recent spatangoids), and these are likely to have borne small, and presumably well-ciliated, spines. In addition the tube feet within a fasciole are not always specialized for funnel-building. For example, *Meoma ventricosus* (Lamarck) has a peripetalous fasciole and *Lovenia elongata* (Gray) has an inner fasciole yet in both species all the aboral tube feet of ambulacrum III are sensory and lack a terminal disc.

The pores that lie within a sub-anal fasciole are associated with funnel-building tube feet, though occasionally an undeveloped tube foot or two may be present along with the funnel-building tube feet. The absence of a sub-anal fasciole does not rule out the presence of sub-anal funnel-building tube feet. These are found in spatangoids, such as *Agassizia scrobiculata* Agassiz and Desor and *Brissaster fragilis* (Düben and Koren), were there is no sub-anal fasciole.

2. There is almost always a pronounced change in the size of the peripodia, marking the change from sensory to funnel-building tube feet. If pores of the sub-anal region are obviously larger than other ambital pores then it is fairly certain that they bear funnel-building tube feet. Similarly for ambulacrum III, if there is a sharp change from very small, apical pores to much larger pores, away from the apex, and a similar, but less pronounced, change from large pores to small pores ambitally, then dorsal, funnel-building tube feet are present.

3. Where the aboral pores in ambulacrum III are so closely spaced as to more or less touch one another, the associated tube feet are modified for funnel-building. Where aboral pores are more widely spaced the associated tube feet may be sensory in function, as in *Maretia* or *Brissus*, or may be used for funnel-building, as in *Brissopsis atlantica* or *Hemiaster expurgitus*.

4. If ambulacrum III is flush with the test surface, or even slightly raised, the associated tube feet are, in most cases, sensory in function. Only *Echinocardium pennatifidum*, of the species examined, have funnel-building tube feet and an ambulacrum that is not sunken. Anterior ambulacra, that are deeply sunken, all possess funnel-building tube feet in the spatangoids examined. This is not true for holasteroids, such as *Cardiaster* and *Infulaster*, where the deeply sunken ambulacrum is more or less vertical over much of its length. The pore morphology and arrangement tend to suggest that dorsal tube feet of the anterior ambulacrum in these species were sensory. A slightly depressed anterior ambulacrum may have either sensory or funnel-building tube feet.

5. Unipores rimmed by an attachment area, unipores with an extensive periporal area, and constricted unipores are all associated with funnel-building tube feet. In nearly all cases broad-rimmed unipores are associated with sensory tube feet. The only exception found was again in *E. pennatifidum*, where broad-rimmed unipores support both sensory and funnel-building tube feet. Partitioned isopores with an axially positioned neural canal, found in Recent spatangoids that were examined, all bear funnel-building tube feet. This, however, is unlikely to be true in more primitive echinoids. For example, in the holasteroid *Infulaster*, partitioned isopores are found in ambulacrum III. These do not vary in size or construction along most of the ambulacrum and are similar in size and shape to other ambital isopores. They are likely to have borne sensory tube feet.

Clearly then, it is not always possible to be certain as to whether a particular pore was associated with sensory or funnel-building tube feet. However, by considering the pore structure and arrangement and the size variation of pores over the test it is often possible to be reasonably certain of the type of tube foot supported.

THE EVOLUTION OF TUBE FEET AND ITS ADAPTIVE SIGNIFICANCE

Most workers are agreed that irregularity in echinoids evolved independently in two or more groups (see Durham 1966 for a comprehensive review). Tube feet in different groups of Recent irregular echinoids are often morphologically very different. They are, however, rarely, if ever, preserved in the fossil record and their evolution can be interpreted only through a study of the ambulacral pore morphology. Kier (1974) has realized this and has followed carefully certain evolutionary trends in pore morphology. He has interpreted these changes in terms of functional modifications of the associated tube feet. It is now possible to identify the probable evolutionary advances in tube foot morphology in rather more detail and to enlarge upon the adaptive significance of the changes that occur.

The pygasteroids are a short-lived group thought by Durham (1966) to have originated from a pedinoid ancestor. Members have both oral and aboral partitioned isopores with a laterally positioned neural canal in which the pores diverge. Both oral and aboral tube feet were probably suckered (Smith, 1978*a*). Pygasteroids appear to have retained the suckered tube foot and ampulla of regular echinoids with little or no modification.

The holectypoids, which originated either from a diadematoid ancestor (Mortensen 1948; Devries 1960) or from a pseudodiadematoid ancestor (Durham 1966), are represented by only two living genera. The tube feet of *Echinoneus cyclostomus* are only slightly modified with respect to those of non-cidaroid regulars. The tube foot still retains a septum, a rosette and frame, and a sucking disc. However, the disc muscles are well developed and the ampulla is squatter than would be expected. Both oral and aboral tube feet are suckered. The development of disc muscle fibres may be linked with the size of the disc which is very much smaller than the sucking disc in tube feet of regular echinoids. The pore morphology and arrangement in the earliest holectypoid genus *Holectypus*, is more or less identical to that found in the Recent *Echinoneus*. It seems safe to assume that the tube feet and ampullae of *Holectypus* were similar to those of *Echinoneus* and that little morphological change has occurred in the tube feet of the holectypoids.

The galeropygoids, which gave rise to both the cassiduloids and the disasteroids are believed to have originated from an acrosaleniid ancestor (Mintz 1968), though Devries (1960) suggested a diadematoid ancestry and Markel (1978) rules out a stirodont ancestor. Both *Galeropygus* and *Hyboclypus* have partitioned isopores aborally which presumably bore simple, suckerless, and somewhat flattened tube feet. Highly specialized respiratory tube feet were quickly evolved in the early cassiduloids. The primitive *Clypeus* species *C. michelini* Wright has compact anisopores with little separation of the two pores. The associated tube feet may have had a narrow partitioned region developed between the pores. In later species of *Clypeus* conjugate anisopores are highly developed and often extremely elongate. This trend towards more elongate anisopores represents a change from tall and slender tube feet to short and elongate tube feet. This helps maintain the efficiency of the tube feet as they shorten to become better protected following the adoption of an infaunal mode of life. It does not necessarily mark the development of more efficient respiratory tube feet.

Partitioned isopores with an axially positioned neural canal are found on the oral surface of galeropygoids and Jurassic cassiduloids. These are oval and have a narrow attachment area and a slender interporal partition. Although these isopores superficially resemble isopores of peristomial plates in some regular echinoids, the large area of pore space suggests that the associated tube feet were highly active and were most likely similar to those found in Recent cassiduloids. Kier (1974) has noted that the partition in oral isopores of cassiduloids is gradually lost during the late Cretaceous and early Tertiary.

Cassiduloids and holectypoids are known to use their tube feet in feeding (Thum and Allen 1976; Gladfelter 1978; Rose 1978). They pick up and transport suitable particles by means of their suckered tube feet and not, as suggested by Kier (1974), by means of mucous adhesion and prehensile grip, as is found in spatangoids. Because of the diameter of their disc, these tube feet are capable of handling only coarse sand and gravel-sized particles. Jesionek-Szymanska (1978) has shown that galeropygoids probably became irregular following a change in feeding habits and the loss of the dental apparatus. Galeropygoids may therefore have evolved from an ancestor which inhabited a suitably coarse substrate where organic-rich particles could be selectively ingested without grazing. A similar life style has been postulated for the unrelated pygasteroid *Plesiechinus ornatus* (Buckman) which is known to have inhabited oncoid-rich substrates (Smith 1978*a*). Cassiduloids and disasteroids rapidly evolved from galeropygoids and all quickly diversified to cope with life in substrates of lower organic content where large quantities of substrate had to be ingested. This necessitated the development of a posterior sulcus or the posterior migration of the periproct to deal with the increased discharge of sediment from the anus. Holectypoids appear to have evolved in parallel and likewise rapidly adapted to feeding by sediment swallowing.

The disasteroids evolved from a galeropygoid ancestor (Mintz 1968). Early forms, such as *Pygomalus ovalis* (Leske) and *Pygorhytis ringens* (Agassiz), have small partitioned isopores on both oral and aboral surfaces. They therefore lacked specialized aboral respiratory tube feet. The morphology and arrangement of partitioned isopores on the oral surface is very similar to that found in contemporary galeropygoids and cassiduloids, as pointed out by Kier (1974). Like cassiduloids, the associated tube feet were almost certainly suckered and the ampullae cylindrical. These disasteroids presumably fed on substrate particles collected and transported by their tube feet as did other Jurassic irregulars.

It therefore appears that all groups of primitive irregular echinoids relied on suckered tube feet for collecting the particles on which they fed. If this were indeed the case then the early irregulars would have been capable of handling only relatively coarse substrates leaving vast areas of the sea floor unexploited.

The holasteroids, which were descended from the disasteroids (Mintz 1968), had developed aboral linked isopores indicating that respiratory tube feet were present. These tube feet were presumably relatively tall and narrow. Kier (1974) has noted that, in the disasteroid–holasteroid lineage, there is a progressive reduction in the number of isopores surrounding the peristome and a corresponding increase in their size. In echinoids such as *Echinocorys*, *Infulaster*, and *Holaster* the partitioned isopores with an axially positioned neural canal, present around the peristome, are large. The associated tube feet must have terminated in a considerably larger disc than tube feet in any other position. The change towards increasingly large phyllode isopores, which started some time during the early Cretaceous, almost certainly marks the change from suckered tube feet to tube feet which relied on mucous adhesion. This innovation permitted holasteroids to feed on finer substrates than had hitherto been possible.

Spatangoids also evolved from a disasteroid ancestor (Devries 1960; Fischer 1966; Mintz 1968). The presence of more or less identically structured penicillate tube feet around the peristome in all spatangoid families examined by Lovén (1883) or by the author, as well as in the holasteroid *Urechinus*, suggests that penicillate tube feet may have already evolved in the disasteroids prior to the evolution and diversification of the holasteroids and spatangoids. Indeed it is quite possible that the development of mucous adhesive tube feet, permitting irregular echinoids to colonize fine-grained substrates, was a major factor giving rise to this rapid burst of evolution. In the spatangoids, funnel-building tube feet were evolved as an adaptation for an infaunal mode of life within a fine substrate. Fossil holasteroids, examined by the author, do not appear to have developed funnel-building tube feet. This adaptation permitted spatangoids to feed on sub-surface sediments inaccessible to the holasteroids.

Funnel-building tube feet can be arranged into a morphological series which may represent a true evolutionary progression. The simplest funnel-building tube feet differ from suckered tube feet in having a greater number of rosette elements. These elements may be broad and flat but more commonly they are elongate and narrow. In some the rods may be extremely long and slender and are connected by a web of connective tissue to form a flexible umbrella-like disc. In others the margin of the disc has become indented. The next morphological advance comes with the separation of rosette elements and the penetration of the lumen into the disc. In the most specialized tube feet the skeletal elements are reduced in size and increased in number while the disc lumen becomes more extensive. The functional significance of this morphological development has been discussed previously. Basically it results in a larger surface area of mucus-producing epithelium and a more flexible disc capable of picking up sediment in a prehensile manner.

Aboral tube feet in all but the anterior ambulacrum are mostly specialized for gaseous exchange in the spatangoids. Respiratory tube feet can also be arranged into a morphological series in which the trend is towards increasing their surface area without increasing their height. Sensory tube feet in holasteroids and spatangoids retain 'juvenile' characteristics seen in the developing suckered tube feet at the apex of some regular echinoids. The developing adapical pores are unipores which later change into isopores by the growth of an interporal partition. They are associated with simple suckerless tube feet. Sensory tube feet in irregulars are probably the result of paedomorphism.

The origin of the clypeasteroids is under some dispute. Durham (1966) argues for their derivation from a holectypoid ancestor whereas Phelan (1977) favours a cassiduloid ancestor. Recent work on the comparative morphology of the lantern and teeth of cassiduloids (Markel 1978) supports the view that clypeasteroids were derived from the cassiduloids. The minute, suckered tube feet of clypeasteroids bear a striking resemblance to the suckered tube feet of cassiduloids, especially to the small ambital tube feet where the rosette is much reduced. Ambital unipores of cassiduloids are also very similar to unipores of clypeasteroids (cf. Pl. 5, fig. 1 and Pl. 4, fig. 3). It would be a relatively simple step to multiply the number of tube feet and ampullae arising from each lateral branch of the radial water vessel to derive the simplest clypeasteroid arrangement. The reduction in size and increase in number of tube feet in clypeasteroids is an adaptation to cope with feeding in the finer sands. Although their tube feet still rely on suction for collecting particles, the small size of the terminal disc permits sand-sized particles to be handled. Clypeasteroids were therefore able to evolve and diversify in a niche previously inaccessible to cassiduloids.

A summary of the postulated evolutionary changes that have occurred in post-Palaeozoic echinoids is given in text-fig. 15.

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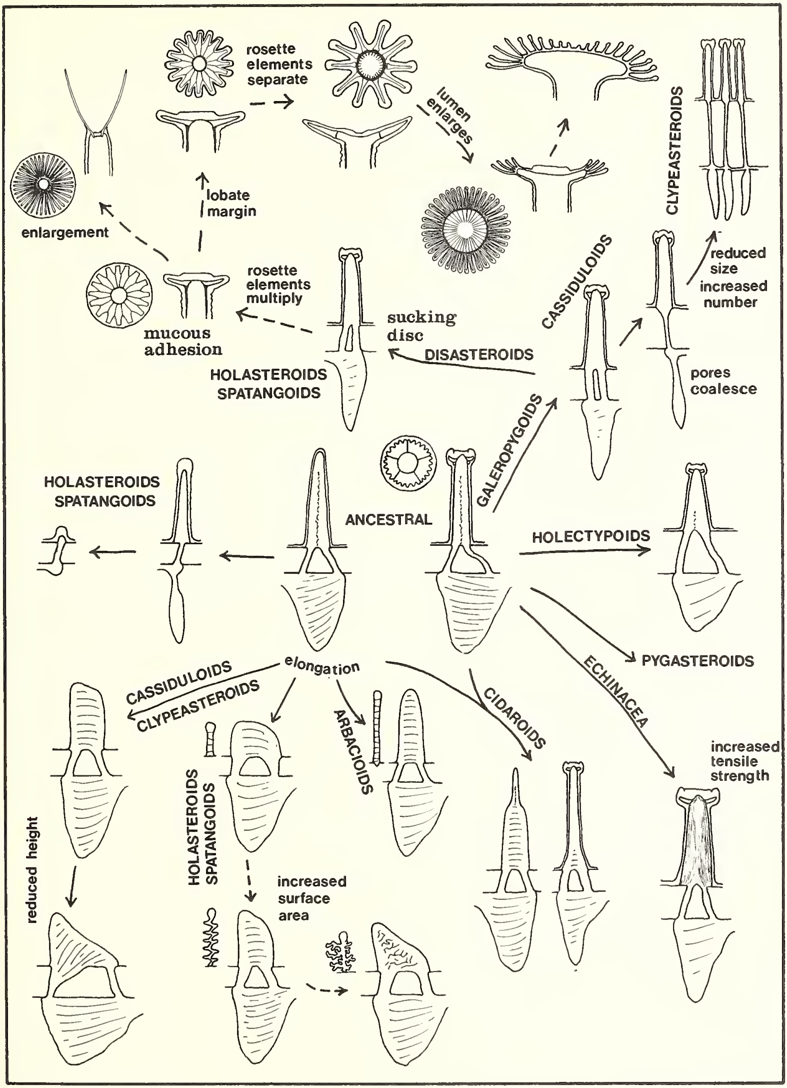

TEXT-FIG. 15. Evolutionary diversification of tube foot structure in post-Palaeozoic echinoids. Dashed lines indicate morphological series. Tube feet/ampullae not to scale.

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A REVISION OF THE TURKISH MIOCENE HOMINOID *SIVAPITHECUS METEAI*

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ABSTRACT. A new specimen of fossil ape is described from the late Miocene of Turkey. It consists of a complete palate and lower face, with much of the nasal and zygomatic regions preserved and part of the right orbit. It is considered to belong to the same species as the previously described *Ankarapithecus meteai* from the same deposits, and it is confirmed that the affinities of this taxon are with the genus *Sivapithecus*. Detailed comparisons with the other species of *Sivapithecus*, however, demonstrate that it is different from them, and its synonymy with *S. indicus* proposed by Simons and Pilbeam (1965) is therefore rejected. It now appears that the genus *Sivapithecus* contains three and possibly four species which have only minor differences from *Ramapithecus* species. The generic distinction is nevertheless retained on the basis of morphological differences in I^1, premolars, and mandibular and maxillary robustness. The possibility of relationship between *S. meteai* and the orang-utan, based on similarities in the maxilla and lower face, is discussed.

PALAEONTOLOGICAL work in Turkey is providing evidence for the existence of several fossil ape species living there in the Miocene. This note describes one of these, *Ankarapithecus meteai* Ozansoy, 1957, based on the type mandibular fragment described by Ozansoy (1957, 1965) and a new specimen found in 1967 but described here for the first time. Both specimens were discovered in the Middle Sinap series in Turkey, the mandible from the lower level of the Middle Sinap and the new specimen, which consists of a complete palate and lower face, from the upper level.

The Sinap series was named by Ozansoy (1955) for a sedimentary sequence nearly 100 m in thickness to the north of the village of Yassörien (4 km north-west of Kazan, 55 km north-west of Ankara, Central Anatolia). The lowest deposits in the sequence appear to lack *Hipparion* (Ozansoy 1965), but they are only sparsely fossiliferous. The middle Sinap beds have produced an abundant fauna which indicates a middle Vallesian age for the deposits.

The type mandible of *A. meteai* consists of a left tooth row, P_4–M_3, associated with a symphysis with the crowns of left C–P_3 and right I_2–C. The rest of the body of the mandible was originally present but was broken in the course of excavation, so that there is no doubt that the teeth belong to one individual. The incisor and canines are low-crowned teeth, similar in size to the largest specimens of *Sivapithecus indicus* from the Siwaliks (Simons and Pilbeam 1965) and with the upper part of the range of variation of *Dryopithecus macedoniensis* from Greece (de Bonis *et al.* 1974, 1975). The P_4 is larger than known *S. indicus* specimens, as are M_1 and M_3, but they are only just beyond the range of variation for the Asian species, and M_2 is exceeded in size by at least two specimens. All the molars are within the 95% confidence limits of the *S. indicus* sample: see Table 1. Molar morphology is practically identical to that of *S. indicus*, and on these grounds Simons and Pilbeam (1965) discounted the slight size difference and synonymized *A. meteai* and *S. indicus*.

There has been no reason to question the synonymy of Simons and Pilbeam (1965) until recently, when new evidence for the presence of a large dryopithecine from Greece has been provided by French workers (de Bonis *et al.* 1974, 1975; de Bonis and Melentis 1977*a*). This dryopithecine was first named *D. macedoniensis* but, on the recovery of a nearly complete palate, it was reassigned to a new genus, *Ouranopithecus*. *O. macedoniensis* is a thick-enamelled form, very similar to *S. indicus* in molar morphology but bigger and with a distinctive morphology of the P_3. The incisors are relatively broad mesiodistally, low crowned, and more robust than those of *S. indicus* (Tattersall and Simons 1969). The I^1 is very much bigger than I^2 and the canines are very robust. The palate is relatively very broad, more so than in *S. indicus*, and the diverging mandibular tooth rows are similarly wider

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TABLE 1. Comparison of lower molar sizes between *Ankarapithecus meteai*, '*Ouranopithecus macedoniensis*', and *Sivapithecus indicus* (data for *S. indicus* is taken from Simons and Pilbeam, 1965).

		A. meteai	*S. indicus*		'*O. macedoniensis*'	
			Mean	95% confidence limits	Mean	95% confidence limits
M_1	md*	12·9	11·6	10·0–13·3	14·5	10·4–18·6
	bl*	12·0	10·6	9·7–11·5	13·7	9·1–18·3
M_2	md	15·9	14·2	12·2–16·2	16·0	12·8–19·2
	bl	14·2	12·8	11·2–14·4	15·0	11·7–18·3
M_3	md	15·8	14·8	13·0–16·7	18·3	13·5–23·1
	bl	14·3	12·6	10·6–14·6	15·5	11·5–19·5

* md signifies mesiodistal length and bl buccolingual breadth. All measurements are in millimetres.

apart than in *S. indicus*. The mandibular symphysis and body are deeper and more gracile in *O. macedoniensis* than in *S. indicus*.

The similarity of the *A. meteai* mandible to the new Greek specimens led one of us (Andrews 1976) to group them in one species. As *meteai* has priority over *macedoniensis*, and as it was considered that the new species was simply a larger version of *S. indicus*, the resulting name used was *S. meteai* (Ozansoy 1957). The subsequent description of a nearly complete palate from Greece (RPL 128, de Bonis and Melentis 1977*b*), and its comparison with the new and even more complete palate and lower face from similar-aged deposits in Turkey, raises a number of interesting questions, for example:

1. Is the new palate attributable to *A. meteai* which is from the same series of deposits in Turkey?
2. Is the Turkish hominoid the same as *S. indicus* or *O. macedoniensis* and are these two taxa themselves justified?
3. Does this and other more complete material throw any light on the relationships of the fossil species with any of the living species of ape or with man?

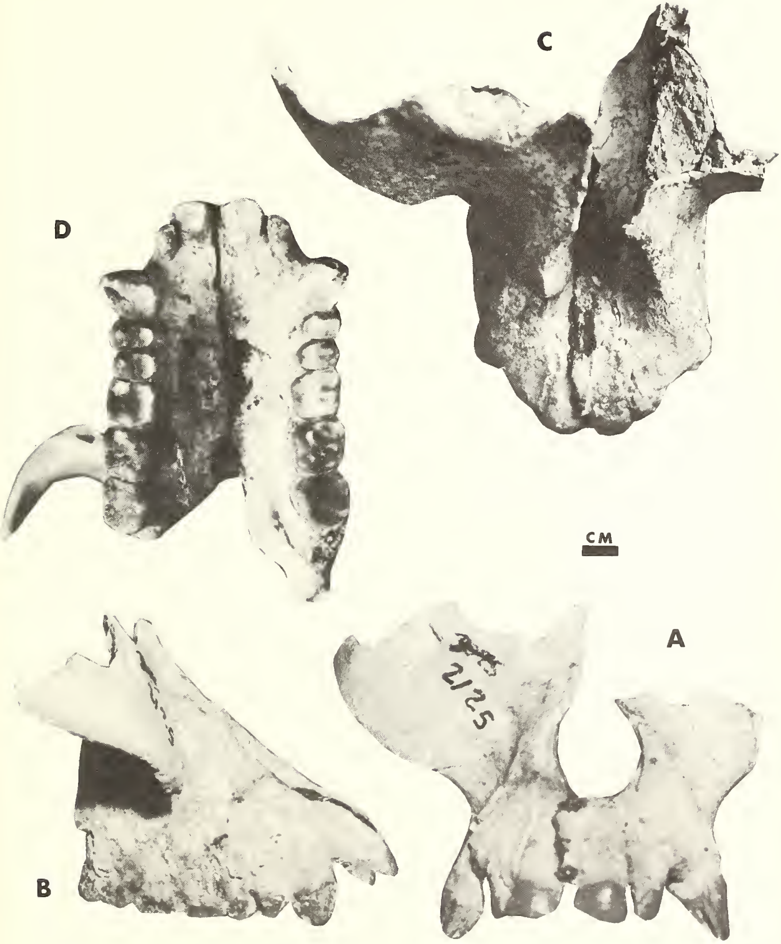
The new palate is registered MTA 2125 and is housed at the Maden Tetkik ve Arama Enstitüsü in Ankara, Turkey.

DESCRIPTION OF NEW SPECIMEN

MTA 2125 consists of a palate with much of the lower face including part of the right orbit at the right zygomatic process of the maxilla. The palate contains the complete dentition, and the alveolar processes are complete on both sides except for a small portion missing posteriorly on the right side. The left palatal process of the maxilla is complete but the right side is broken medio-posteriorly. The right nasal, orbital, and zygomatic processes of the maxilla are complete while, on the left side, the superior and posterior portions are broken away. The nasal bones are missing but, apart from that, the nasal aperture is completely outlined, and the inferior and medial walls of the right orbit are present in two regions. The base of the right zygomatic is preserved, so that the whole of the right lower face is present. There are fresh breaks along the limits of the parts preserved on the right side, so possibly more of this specimen may yet be found. The specimen is shown in text-figs. 1 and 2.

Maxilla

The most striking feature of the maxilla, MTA 2125, is the great development of the zygomatic region. This is preserved intact on the right side (text-fig. 1). The root of the zygomatic process is situated relatively posteriorly, above M^2, and it is sharply angled, passing directly laterally and slightly anteriorly before passing posteriorly into the zygomatic arches. This is best seen in top view (text-fig. 1C). Between the zygomatic process of the maxilla and the alveolar and nasal processes there is a very deep canine fossa, a product of the sharp



TEXT-FIG. 1. Specimen MTA 2125. A, frontal view; B, view from the right side; C, superior view showing the inferior surface of the right orbit and the matrix filled left maxillary sinus; D, palatal view.

angulation of the zygomatic rather than, as is more usual, of the compression of the anterior part of the face. This specimen therefore has the unusual combination of a flat upper face, resulting from the flattened zygomatic processes, and a projecting snout. The latter is partly the result of the posterior position of the zygomatic processes, but is also emphasized by the high degree of premaxillary prognathism. This is indicated by two measurements in Table 2, the projection in a horizontal plane of the premaxilla and maxilla in front of the lower edge of the zygomatic processes, and the length of the premaxilla from alveolare to nasospinale.

The bizygomatic width of the face could be estimated by measuring from the right side of the process to the midline and doubling (text-fig. 1A) and the resulting value of 155·2 is very high for a primate of this size. It is within the range for male gorillas and is intermediate between male and female orang-utans. Similarly the depth of the zygomatic process, which was estimated by measuring the distance between the lowest point on the lower border of the orbit and the base of the zygomatic process, giving a value of 39·5 mm, is only matched by male gorillas and orang-utans. The flattened zygomatic region of the face is therefore both very wide and very deep, and this is coupled with a long lower face due to the projecting snout. It does not, however, appear to be coupled with a long upper face, for the nasal bones are short, and the nasal height, estimated from the distance from nasospinale to the superior break of the orbital process of the maxilla, which was undoubtedly only a few millimetres short of nasion, has a minimum value of 66·5 mm. This is below the range of variation of the gorilla, above that of chimpanzees, and intermediate between male and female orang-utans.

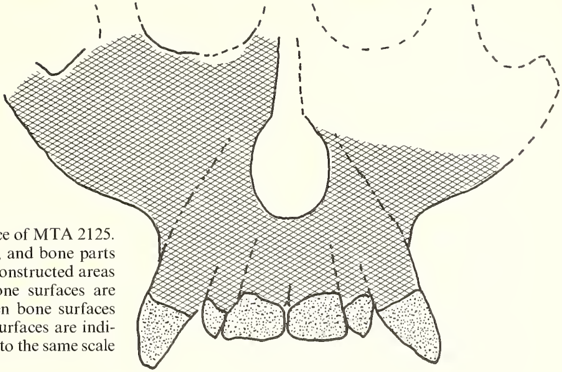
The right nasal bone, which is missing but which has been broken off along the nasomaxillary suture, was a short and narrow bone (text-fig. 1A). The maximum width of the bone, from the nasomaxillary suture to the midline, is 5·5 mm, so that the basal width across the nasal bones can be estimated as 11·0 mm. The nasal bones tapered sharply towards nasion (text-fig. 1A) and although the nasal process is broken just short of the maxillofrontal suture it would appear that they narrowed almost to a point. This resembles the condition found in all of the living great apes and is closest to the orang-utan, in which the nasal bones are narrower at the base as well, but it differs sharply from the condition seen in the African early Miocene apes. All three species of *Proconsul* (Le Gros Clark and Leakey 1951; Pilbeam 1969) have long, fairly broad, and almost parallel-sided nasal bones (Whybrow and Andrews 1978). The length of the nasal bones in MTA 2125, from the base of the nasomaxillary suture to the break just short of the nasofrontal suture, is 31 mm, and this compares with similarly measured minimum lengths of 46 mm for *P. major* (Pilbeam 1969) and 34 mm for *P. nyanzae* (Whybrow and Andrews 1978). In the same way the estimated nasal height of 66·5 mm for MTA 2125 is well below that of both *P. nyanzae* and *P. major*, so that its nasal region is considerably shorter than in comparable-sized species of *Proconsul*.

Consistent with this is the relatively broad nasal aperture in MTA 2125. Is is almost as broad as it is long (Table 2) and is unlike the long narrow apertures of the African early Miocene apes (Andrews 1978). It is, however, very similar to the nasal aperture of the recently described *O. macedoniensis* palate from Greece (RPL 128, de Bonis and Melentis 1977) which has slightly larger nasal aperture dimensions of approximately 25·8 mm broad and at least 27·0 mm high. Among the living great apes this combination of narrow tapered nasal bones and broad nose appears most commonly in chimpanzees; orang-utans tend to have very narrow nasal bones but they also have relatively high narrower noses, while gorillas often have very broad nasal bones and rather broader noses.

The position of the right orbit relative to the midline permits some approximate measurements to be made of the orbits on MTA 2125. The right orbit has an estimated minimum breadth of 32·5 mm, but its height is unknown. The most medial point of the right orbital border is 6 mm from the midline, so that the estimated minimum breadth between the orbits is approximately twice this (Table 2). The distance of the most medial

TABLE 2. Facial measurements of MTA 2125.

Bizygomatic width	155·2
Alveolare to nasospinale	19·5
Nasal height (minimum)	66·5
Nasal aperture breadth	23·0
height	24·5
Horizontal projection of alveolare from the plane of the zygomatic processes	53·0
Orbit breadth	32·5
Minimum biorbital breadth	12·0
Biorbital breadth across lacrymal crests	15·2



TEXT-FIG. 2. Reconstruction of the face of MTA 2125. The drawing is based on text-fig. 1A, and bone parts present are shown stippled, while reconstructed areas are left blank. Intact or sutural bone surfaces are shown by a heavy black line, broken bone surfaces left blank, and reconstructed bone surfaces are indicated by a dotted line. The drawing is to the same scale as text-fig. 1.

and superior point of the lacrymal fossa from the midline is 7·6 mm, so that the distance between the orbits across these two points is 15·2 mm (Table 2). This compares with values ranging from 14·6 to 24·8 mm for the three species of *Proconsul* (Whybrow and Andrews 1978) using the same points and is less than the values for male chimpanzees and gorillas, although it just comes within the range given for female chimpanzees (Pilbeam 1969). It is well within the range for orang-utans, and there is no doubt that, like the orang-utans, the orbits of MTA 2125 were set very close together. This is illustrated in text-fig. 2, which shows a reconstruction of some of the missing parts on the left side drawn in to match the equivalent parts on the right.

The alveolar processes of the maxilla are straight and almost parallel. The external borders of the palate diverge posteriorly so that the breadth across the M^2 exceeds that across the canines (see Table 3). The Greek palate RPL 128 (de Bonis and Melentis 1977*b*) resembles the Turkish one in this respect except that over all the palate of MTA 2125 is 6–8 mm narrower than RPL 128. Both specimens contrast with *P. major*, in which the tooth rows converge posteriorly as in male great apes, although the degree of sexual variation in this feature is so great as to render the difference insignificant (Pilbeam 1969). Internally also the breadths between endomolaria in MTA 2125 and RPL 128 are almost identical to the bicanine width, but the palate of MTA 2125 again appears narrower over all than the Greek palate RPL 128 (see Table 3).

It was not possible to measure the length of the palate because posteriorly the central part of the palate is missing. However, the length of the alveolar process could be measured on the left side, and this gives an approximation to palate length. It has very similar dimensions to the alveolar process of *P. major* and as a result the internal palate shape, as indicated by the endomolare breadth divided by the length of the alveolar process, is similar in the two specimens (Table 3). The palate from Greece, RPL 128, appears much broader (see Table 3), but a new palate of *S. indicus* from Pakistan (Pilbeam *et al.* 1977) has similar proportions to MTA 2125. The palate of MTA 2125 is rather shallow, as in most fossil apes, approximately 11·5 mm at the level of M^1. The greater palatine foramina are set well forward alongside the crowns of M^3.

TABLE 3. Palatal measurements of MTA 2125 compared with the roughly contemporary palate from Greece (RPL 128, de Bonis and Melentis 1977*b*) and the palate of *Proconsul major* from early Miocene deposits in Uganda (UMP 62-11, Pilbeam 1969).

	MTA 2125	RPL 128	UMP 62-11
External breadth across the canines	59·0	64·0	66·5
External breadth across the M^2	61·9	70·8	62·5
B at M^2/B at C × 100	105·0%	110·6%	94·0%
Endomolare breadth (M^2)	34·4	40·0	33·4
Length of alveolar process	93·5	(89)	95·8
Endomolare B/L alveolar process × 100	36·8%	45%	34·9%

The alveolar processes of MTA 2125 appear to be fairly robust, but it has not been possible to assess their degree of inflation because the matrix has not yet been removed from the maxillary sinuses. The extent of the floor of the left maxillary sinus is shown, in text-fig. 1c, to be limited in extent, not passing into either the zygomatic processes or the posterior tuberosities of the alveolar processes, even though both these elements are relatively large. The floor of the maxillary sinus extends anteriorly only as far as the distal half of M^1 rather than to P^4 as is normally the case. Even the relatively restricted maxillary sinus of *P. major* (Pilbeam 1969) extends anteriorly to the P^4 and passes also into the zygomatic processes and the alveolar tuberosities.

Dentition

The upper central incisor on MTA 2125 is a large spatulate tooth (text-fig. 1d). It is similar in size to the I^1 of *S. indicus* but is slightly stouter and is much lower crowned. The degree of wear on the incisors, however, is so great that the height measurements, given in Table 4, must be considerably lower than on unworn teeth. The I^1 of *S. darwini* from Pasalar in Turkey is smaller and even more high crowned than *S. indicus* (Andrews and Tobien 1977). The I^1 on MTA 2125 is most similar to that of the Greek palate, RPL 128 (de Bonis and Melentis 1977), and comparative measurements for this specimen and for *S. indicus* are given in Table 4. Both the Greek and the Turkish specimens have low-crowned incisors, and in both the I^1 is very much larger than the I^2. This is particularly true of MTA 2125, in which I^1 is more than twice the length of I^2, but the relation of I^1 to I^2 on RPL 128 approaches this, with an index value ($I^1/I^2 \times 100$) of 179%. The incisors of the African apes and most dryopithecines are closer to each other in size, with I^1/I^2 index values ranging between 120% and 150% (Andrews 1978), and only in the orang-utan among living apes is the I^1 nearly twice the size of I^2.

The canine of MTA 2125 is also very low crowned (text-fig. 1d). In crown area it is slightly bigger than in *S. indicus*, but in crown height it is smaller than in most fossil ape species. It is also considerably more robust than in *S. indicus* and *S. darwini*. Indeed, it is more robust and low crowned (with one exception) than in any other fossil or living ape known at present, the index values for breadth against length and length against height being 89% and 95% respectively (Table 4). The exception again is the Greek palate (RPL 128), in which the canine index values are 87% and 99% respectively (Table 4). In both specimens the canine is considerably worn, so that the height measurement may be underestimated, but the other dimensions are not affected. Little morphological detail can be seen because of the wear, but both specimens have an unusually deep mesial groove. In many apes the mesial groove is obliterated by wear at a fairly early stage in dental wear, but on these two specimens, even though they are both heavily worn, the mesial groove is still prominent.

Although the incisors and canines in the Turkish and Greek palates (MTA 2125 and RPL 128) are practically identical in size and morphology, they have rather different proportions to their respective postcanine teeth. The molars and premolars of MTA 2125 are considerably smaller than in RPL 128, so that the ratios between the anterior and posterior teeth are much higher. This can be illustrated by comparing the cross-sectional areas of the canine and the first molar. In MTA 2125 the C is larger than M^1, the index ($C/M^1 \times 100$) being 122%, and in RPL 128 it is smaller, the index being 95%. At first sight such a difference is reminiscent of sexual variation. The C/M1 ratio is one often used to measure sexual dimorphism, as it relates the size change of the dimorphic canine to the more stable M1, but in this case the canines are identical in size and it is the

TABLE 4. Measurements of detition of MTA 2125 compared with RPL 128 from Greece (de Bonis and Melentis 1977*b*) and mean values for *Sirapithecus indicus* (sample sizes are given in brackets).

	Length*			Breadth*			Buccal height		
	MTA 2125	RPL 128	*S. indicus* mean	MTA 2125	RPL 128	*S. indicus* mean	MTA 2125	RPL 128	*S. indicus* mean
I^1	11·6	11·6	11·6 (1)	9·4	9·5	8·9 (1)	9·4	8·0	13·1 (1)
I^2	5·5	6·5	—	6·6	6·0	—	7·1	4·8	—
C	14·9	14·9	15·5 (4)	13·2	13·0	10·9 (4)	15·7	13·1	20·5 (2)
P^3	8·9	9·7	9·0 (3)	12·0	13·7	11·9 (3)			
P^4	7·8	9·2	7·6 (4)	12·4	14·4	11·9 (4)			
M^1	11·8	13·7	11·4 (7)	13·7	14·8	12·4 (7)			
M^2	13·5	15·0	12·5 (7)	14·3	16·3	14·2 (7)			
M^3	14·5	14·6	12·2 (4)	14·7	15·7	13·4 (4)			

* Lengths are mesiodistal and breadths are buccolingual, except in the case of the canine, in which the length is the maximum length of the crown and the breadth is measured perpendicular to the maximum length.

molars that are different. As such it appears that the Turkish palate must represent a smaller individual with relatively larger canines than in the Greek palate.

The upper premolars on MTA 2125 are almost equal in size, the P^3 being slightly smaller than the P^4. The P^3 is buccally elongated so that it has a bluntly triangular outline: the midline length of P^3 is 7·8 and the lingual length is 6·9, comparing with the buccal length (Table 4) of 8·9. In these dimensions the P^3 is very similar to the P^3 of *S. indicus* and *S. darwini*, except that on the former the mesiobuccal angle of the crown projects mesially into a beak-like process which is absent on the Turkish specimens. They all differ from the Greek palate (RPL 128) on which the P^3 is considerably larger, the mesial and distal borders of the crown are almost parallel, and the P^3 is exactly the same size as the P^4. The P^4 on MTA 2125 is almost identical to that of *S. indicus* and *S. darwini* and again differs from the P^4 of RPL 128 in being considerably smaller (Table 4).

The upper molars of MTA 2125 are flattened by wear (text-fig. 1D). Almost all the enamel has been worn away from M^1 and dentine exposed; M^2 has dentine exposed mesiolingually and P^4 lingually; and the enamel on M^3 is worn flat but with no exposure of dentine. The molars have squared outlines, with large areas of contact with each other, and they increase in size from M^1 to M^3. Little crown detail can be seen on M^1 because of the wear, but M^2 has a well-defined crista obliqua and no traces of lingual cingulum. The protocone becomes progessively bigger on M^1 to M^3, and the distal cusps are progressively reduced, but this has not resulted in any reduction in size of the M^3, which is both the longest and the broadest tooth in the tooth row (text-fig. 1D).

In both size and morphology the molars of MTA 2125 correspond most closely to those of *S. indicus* and *S. darwini*. There are, however, a few differences, particularly in the molar proportions and the squared outline of the molars. The M^1 of MTA 2125 is at the top of the size range of *S. indicus* and *S. darwini* but is smaller than the M^1 of the Greek palate RPL 128; but the M^3 approaches the latter in size and is very much bigger than the M^3 of *S. indicus* and *S. darwini*, on both of which the M^3 is smaller than M^2 (Table 4). An enlarged M^3 is an unusual feature in dryopithecines, and only occurs in one other group, *Rangwapithecus* species from the early Miocene of East Africa (Andrews 1978), but with only one specimen it is difficult to assess the significance of this character in the Turkish specimen. The squared appearance of the molars also differs from the condition in both *S. indicus* and *S. darwini*, as well as the Greek palate RPL 128, all of which have molars with more rounded crown outlines and with some degree of distal abbreviation of the crowns on M^2 and M^3. Again, the significance of this difference is uncertain because of the small number of specimens, although the pattern is well established for *S. indicus* and *S. darwini*.

Association of MTA 2125 with the type specimen of Ankarapithecus meteai

A number of palatal and mandibular dimensions have been compared with each other to assess the degree of similarity between MTA 2125 and the mandible of *A. meteai*. These include intercanine, interincisor (I2), and intermolar widths plotted against tooth row length for samples of chimpanzees, gorillas, and orang-utans. Comparing the Turkish mandible and palate with the samples of living apes, the over-all shape and relative breadths of mandible and palate are consistent with each other even to the extent of belonging to the same sex (probably male). In other words, the over-all similarity in shape between the fossil mandible and maxilla is greater than would occur within one species of living ape if different sexes were compared. The degree of difference displayed by the five mandibles and one palate from Greece (de Bonis *et al.* 1974, 1975; de Bonis and Melentis 1977*a*) confirms that they also belong to a single species, and it also suggests that the palate RPL 128 could be a female, for it is closer to the small mandible (RPL 54) than to the three larger ones (RPL 55, 56, and 75). This is contrary to the conclusions of de Bonis and Melentis (1977*b*), but a female sex for RPL 128 is also indicated by the relatively broad palate, the posterior divergence of the tooth rows, and the small canine size relative to M1.

Much of the morphological detail in the palate MTA 2125 is also consistent with its association in one species with the mandible of *A. meteai*. The deep symphysis of the mandible is consistent with the very long premaxilla (Table 2) and the degree of alveolar prognathism. The laterally compressed incisor tooth row on the mandible is consistent with the maxillary incisor compression, and the upper and lower I2s are similarly more robust than the I2s of the Greek specimens. The more robust I_2 could also be related to the relatively larger I^1 of MTA 2125, as both I_1 and I_2 occlude against I^1, and only to a lesser extent against I^2, in most ape species. The bilaterally compressed canine in the mandible of *A. meteai* seems to contrast with the exceptionally robust upper canine in MTA 2125, but the same pattern is present in the Greek sample: breadth/length × 100 indices range from 62% to 68% for the lower canines on the four Greek mandibles compared with 87% for the upper canine in RPL 128. The corresponding values for the two Turkish specimens are 71% and 89%. Finally, the upper molars of MTA 2125 are consistent both in size (e.g. M_1–M_3 lengths) and morphology with the lower molars of the *A. meteai* mandible.

RELATIONSHIPS OF THE TURKISH HOMINOIDS

As it appears that the new palate from Turkey is consistent morphologically with the type mandible of *A. meteai*, it remains now to decide on the taxonomic affinities of these specimens. In the course of the description of the palate, comparisons have been made with species of *Sivapithecus* and *Ouranopithecus* as these are clearly the most similar to the Turkish specimens. and these comparisons will now be briefly reviewed.

The upper dentition of MTA 2125 shows many similarities with *S. darwini*, which is known from earlier deposits in Turkey. The incisors and canines, however, are larger and lower crowned and, in the case of the $\underline{C}$, are also more robust. In these features *S. darwini* retains the primitive dryopithecine condition and MTA 2125 has the derived character state (Andrews and Tobien 1977), a state that it shares with *O. macedoniensis*. Similarly in the lower dentition, *S. darwini* retains a number of primitive characters, such as molar cingula, compressed trigonid basins, and elongated M_3 talonids that are changed or absent in the mandible of *A. meteai*. There is therefore little doubt that these specimens represent something different from *S. darwini*.

The Turkish specimens also have many similarities with *S. indicus*. They can, however, be distinguished from *S. indicus* by the following characters: the I^1 is more robust and lower crowned; I^2 is extremely small relative to I^1; $\underline{C}$ is more robust and $\overline{C}$ is less robust; the mesial edge of P^3 is straight, not beaked as in *S. indicus*; P_4 is larger and more molariform; the upper molars increase in size from M^1 to M^3, so that M^3 is large and is not reduced as in *S. indicus*; upper molars are more elongated; and M_3 also is relatively larger than M_1 and M_2 than in *S. indicus*. In all of these characters, except possibly the degree of bilateral compression of the lower canine, *S. indicus* retains what may be interpreted as the ancestral dryopithecine condition, and the new Turkish specimens have the derived condition which is often shared with *O. macedoniensis*. In the case of the lower canines, a bilaterally compressed crown would appear to be the ancestral dryopithecine character state, but it is then associated with a similarly compressed upper canine. It may be that the combination of a compressed lower canine and a very robust upper canine may itself be a derived character state, and it has been shown that there is good evidence for accepting this combination in both the Greek *O. macedoniensis* and in the Turkish specimens. When these differences in proportion and morphology between the Turkish specimens and *S. indicus* are combined with the slight size difference between them, we consider that they are sufficiently distinct to make their allocation to separate species necessary.

This leaves one further species to be considered, *O. macedoniensis*. The palate of *O. macedoniensis* is wider than in MTA 2125, the tooth rows are more diverging, and the postcanine teeth have different proportions to the incisors and canines. The first two of these differences may be exaggerated by the distortion of the palate in RPL 128, the only maxillary specimen of *O. macedoniensis*, and in any case they are often the product of sexual variation: in modern ape species females have relatively wider and more diverging palates than the males and, as ranges of variation of 10–15% are quite common (Pilbeam 1969), the difference between the Turkish and Greek specimens (9%) could be the result of sexual variation. In this case MTA 2125 with its narrow palate would be at the male end of the range of variation, and RPL 128 towards the female end. However, the third difference appears inconsistent with this, for it has been shown that RPL 128 is larger than MTA 2125 in its postcanine dentition (Table 4) while their canines and incisors are of approximately equal size. In the four most complete mandibles of *O. macedoniensis*, which shows an enormous degree of sexual dimorphism (de Bonis and Melentis 1977*b*), the canine/first molar crown area index has a range of 48–77%, and the equivalent index for the maxilla RPL 128 is 91%. The index for the mandible of *A. meteai* is 95%, well above the highest value for the Greek mandibles, and for the maxilla MTA 2125 the value is 122%, also higher than in the single Greek maxilla. This degree of difference, however, is less than that within single species of living great apes, but the larger first molar of RPL 128 suggests that it came from a larger individual than did MTA 2125 which nevertheless had a relatively larger canine.

There are two minor characters in the dentition that distinguish the Turkish material from *O. macedoniensis*. One of these concerns the distinctive morphology of the P_3 on all of the *O. macedoniensis* mandibles. The P_3 has a triangular outline because of the greatly expanded mesiobuccal part of the crown, and the axis of the crown has rotated transversely so that the distolingual ridge, which is very prominent, runs almost directly lingually and delimits a very prominent distal basin or fovea. This appears to be a unique specialization of the P_3 of *O. macedoniensis*, and distinguishes it from the P_3 on the *A. meteai* mandible, which has retained the primitive condition in common with *S. indicus*. The other feature of the dentition is the enlarged M^3 of MTA 2125, which differs from the primitively reduced M^3 of *O. macedoniensis* and most other fossil apes.

It is concluded that the new Turkish material confirms the distinction at the species level between *A. meteai* and *S. indicus*, contrary to the synonymy proposed by Simons and Pilbeam (1965), but there appears to be no good reason for separating them generically. Similarly *O. macedoniensis* appears conspecific with *A. meteai* and, since *meteai* Ozansoy, 1957 has priority over *macedoniensis* de Bonis *et al.*, 1974, and *Sivapithecus* Pilgrim, 1910 has priority over *Ankarapitheicus* Ozansoy, 1957, and *Ouranopithecus* de Bonis and Melentis 1977*b*, the name for the Greek and Turkish material is *S. meteai* (Andrews, 1976). This shares with other species of *Sivapithecus* the suite of derived characters mainly related to the thick enamel on the molars (Andrews 1976), and superimposed on this are the species-specific characters mentioned earlier. Thus *S. darwini* is within this group but still retains many primitive dryopithecine characters. *S. indicus* and *S. meteai* share a minor suite of derived characters which distinguish them from *S. darwini*, for example the enlarge molar trigonid, reduced M_3, and loss of molar cingula. Finally, *S. meteai* has a further suite of derived characters distinguishing it from *S. indicus*, which retains the primitive condition with respect to these characters, for example low crowned I^1 and C, enlarged I^1 relative to I^2, robust $\underline{C}$ and enlarged P_4. The Greek material of *S. meteai*, with its unique P_3 morphology and relatively small canine, and the Turkish material, with its enlarged M^3 relative to M^2, both have derived conditions relative to each other (and to *indicus*), but it is considered that these characters are of insufficient importance to separate them specifically.

DISCUSSION

The three species of *Sivapithecus* discussed here have a time span of at least five million years. They first appear in the beginning of the middle Miocene, at which time the closely related genus *Ramapithecus* is also first known (Andrews and Tobien 1977), and both genera survive well into the late Miocene. *Ramapithecus* and *Sivapithecus* are also extremely similar in morphology, and it must be questioned whether their recent division into separate subfamilies (Pilbeam *et al.* 1977) is justified by the evidence. Pilbeam gives, as his only reason for distinguishing the Ramapithecinae and the Sivapithecinae, the small and less dimorphic canines in *Ramapithecus*, but even with all the new material that has been described in recent years there is still only one known association of a canine with posterior teeth, on the type specimen of *R. wickeri* (Leakey 1962). Pilbeam's evidence, therefore, must be based on the small number of isolated teeth known for this genus (Andrews and Walker 1976; Pilbeam *et al.* 1977), but isolated teeth must be used with extreme caution because their identification is often doubtful. This is particularly true of the Siwalik specimens, for it is possible that the larger canines that are assigned to *Sivapithecus* may include some *Ramapithecus* specimens, in which case the sample is biased for the very character on which the distinction is being made between the two subfamilies.

The presence of a bias is suggested by the present confusion over the affinities of another supposed species of *Sivapithecus*, *S. sivalensis* (Simons and Pilbeam 1965). This species is very similar in both size and morphology to *Ramapithecus*, and it differs, in fact, only in having very slightly larger canines. For example, the length and breadth dimensions of KNM-FT 46, the only known associated canine of *Ramapithecus*, are 10·0 and 8·5 mm, while the ranges for three specimens of *S. sivalensis* (GSI D 1, GSI D 299-300, and K23/212) are 10·8 to 13·5 and 7·4 to 11·2, lengths and breadths respectively in millimetres. It seems very likely that these specimens could represent the upper end of the range of variation of *R. punjabicus* together with the isolated teeth of similar size, and in this case Pilbeam's (1977) distinction drawn between *Sivapithecus* and *Ramapithecus* disappears.

Ramapithecus and *Sivapithecus* are in fact so similar that it may be questioned whether they should even be retained in separate genera. They share the character complex related to thick enamel on the cheek teeth, which was mentioned earlier as being diagnostic of the *Sivapithecus* Group, and on this evidence alone they may be considered as sharing a common ancestry, and their systematic distinction must depend on the presence in one or both of derived characters not shared by the other. One such difference may be seen in the morphology of I^1, which in *Sivapithecus* species has a massive lingual cingular swelling (Tattersall and Simons 1969) that is interpreted as a derived condition compared with the primitive lingual tubercle present in *Ramapithecus* (Andrews and Tobien 1977). Other differences, on the premolars, are the large size of the lower premolars relative to the molars and the strongly oblique angle of the P_3 with respect to the molar tooth row in *Ramapithecus*: although still primitively single-cusped, as in *Sivapithecus*, the large size and angulation of the P_3 and the large size of P_4 in *Ramapithecus* are interpreted as derived conditions probably related to initial molarization of the premolars, and *Sivapithecus* retains the primitive condition in these characters. Finally, a possible third difference is in the greater robustness of the mandibular and maxillary bodies of *Ramapithecus* (Simons and Pilbeam 1965; Andrews and Walker 1976), but this formerly clear-cut difference is becoming less distinct as more material is added to the collections. As the species of *Ramapithecus* share these three characters and none of the *Sivapithecus* species do so, it may be tentatively concluded that the generic distinction between them can be retained.

In the description of the maxilla and dentition of *S. meteai*, the closest comparisons in most cases were with the orang-utan, and this could indicate some degree of relationship between it and the orang-utan. The significance of the orang-like morphology in *S. meteai* is, however, by no means clear. It has a deep and widely flaring zygomatic process, marked alveolar prognathism that is combined with a short upper face, and a narrow interorbital distance, all of which are characters of the maxilla that are shared only with the orang-utan among hominoid species. The dentition lacks the characteristic secondary wrinkling seen in orang-utan teeth today, but the large I^1 relative to I^2 and the large squared molars are characters shared exclusively with the orang-utan. In contrast to this, the characters shared with the African apes are less impressive: the shape of the nose is more similar to that of the chimpanzee, and the length of the molar teeth, with the large M^3, is closest to the condition seen in gorillas. Some of these characters are also present in the maxillae of *S. indicus* and *Ramapithecus*, but whether all of them are therefore related to the orang-utan or whether the similarity is due to a functional convergence resulting, perhaps, from similar dietary adaptations in similar habitats, is not known at present. *Sivapithecus* species have been considered by many authors in the past (see Simons and Pilbeam 1965 for discussion and references) to represent ancestral orang-utans mainly because the fossils are known in the right place (Asia) and the right time (middle to late Miocene). Such arguments carry no weight in the absence of morphological similarity, but with the evidence of similarity presented here between *S. meteai* and the orang-utan the likelihood must be increased that they are related.

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PLIO-PLEISTOCENE OSTRACODS FROM THE UPPER AMAZON OF COLOMBIA AND PERU

by LESLEY M. SHEPPARD *and* RAYMOND H. BATE

ABSTRACT. An unnamed formation from near La Tagua, Colombia, and the Pebas Beds of Peru contains rich ostracod faunas that provide new information on the environment of deposition and the probable age of the sediments. The ostracods are a mixture of freshwater, brackish, and marine species, from what was essentially a brackish-water environment. Fifteen species, of which nine are new, are described, together with two new subspecies. Three genera—*Botulocyprideis*, *Otarocyprideis*, and *Rhadinocytherura*—are new.

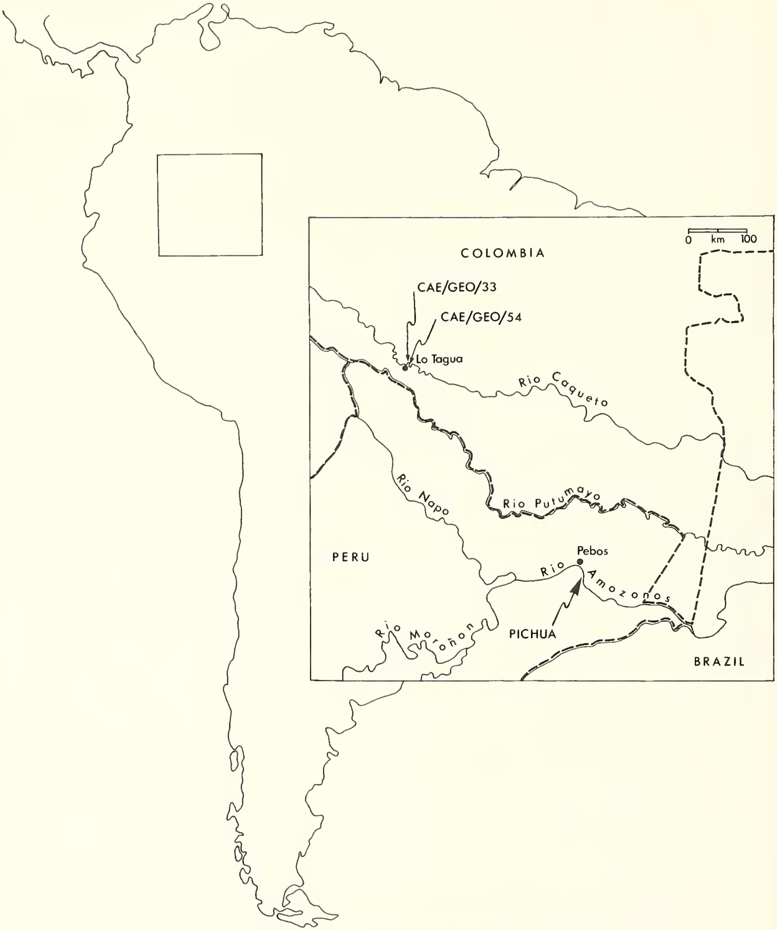
FROM a collection of South American molluscs being examined by C. P. Nuttall three samples of marl were processed for ostracods. The ostracods proved to be an undescribed fauna, and give information concerning the environment of deposition and the possible age of the sediments.

Text-fig. 1 shows the sample localities. The one Peruvian sample, chocolate-brown marl of the Pebas Beds from northern Peru, was extracted from matrix in molluscs collected by Mr. Hauxwell in 1870 from Pichua, just west of Cochaquinàs, approximately 30 miles (48 km) down the Marañon River from Pebas (approx. lat. 3° 23′ N., long. 72° 10′ W.). The two Colombian samples were shelly grey clays from an unnamed sequence collected in 1977 by Michael Eden during the Colombian Amazonas Expedition, Projecto Radargrametrico dell Amazonas, from the Caqueta Basin area of southern Colombia—lat. 0° 05′ N., long. 74° 40′ W.: sample CAE/GEO/54 from the river bank just downstream of La Tagua and sample CAE/GEO/33 from a well about ½ km from the Caqueta River at a depth of 480–560 cm from the surface. The age of the Peru sample is considered by some to be Pliocene (Gardner 1927) although Simpson (1961) regarded the so-called Pebas Beds of the Porto Peter on the Juruá River, Brazil, as being Pleistocene in age or even younger. There are, however, no molluscan genera or species common to the Pebas Beds of Peru and Simpson's locality so it is unlikely that they represent the same formation or are of the same age (pers. comm. C. P. Nuttall). The presence of marine ostracods in the Pebas Beds of Peru makes it unlikely that these beds could be younger than Pleistocene if introduced via a marine transgression.

Gardner (1927) considered the mollusc fauna to be Pliocene in age, and referred to the presence of freshwater ostracods, as *Cypris* sp. associated with the molluscs. Little detailed work has been undertaken on the ostracods of the Upper Amazon—either fossil or Recent—and considerable scope exists for taxonomic studies on the ostracod faunas and their application to the elucidation of the environment of deposition and the correlation of the sediments. The most important published work is that of Purper (1977) who figures ostracods of Pliocene or younger age from the Upper Amazon of Brazil.

All the ostracods described in this paper have been deposited in the British Museum (Natural History), London. All measurements are in mm.

[Palaeontology, Vol. 23, Part 1, 1980, pp. 97–124, pls. 7–13.]



TEXT-FIG. 1. Location map of Peruvian and Colombian samples.

SYSTEMATIC DESCRIPTIONS

Superfamily CYTHERACEA Baird, 1850
Family CYTHERIDEIDAE Sars, 1925
Subfamily CYTHERIDEINAE Sars, 1925
Genus CYPRIDEIS Jones, 1857
Cyprideis purperi sp. nov.

Derivation of name. After Ivone Purper of Universidade Rio Grande do Sul.

Diagnosis. Sulcate species of *Cyprideis* with surface ornamentation of small pits. Seven to nine short anterior marginal spines on free margin of both valves.

Description. Carapace subquadrate in lateral outline, tapering slightly to the posterior, especially in the male dimorph, and with a shallow but distinct dorso-median sulcus. Shell parallel-sided in dorsal view with variously developed anterior marginal borders. Ventral margin convex in juvenile instars, becoming straight with incurvature anterior of the mid-point in adults. Dorsal margin convex with distinct anterior cardinal angle. Surface ornamented with small rounded pits which decrease in size towards valve edges. Anterior margin bears short terminal spines; postero-ventral margin may or may not have terminal spines. Left valve larger than the right. Normal pore canals are of sieve type; hinge and muscle scars as for genus (Pl. 7, figs. 2, 6; Pl. 8, figs. 1, 2). Marginal pore canals, some of which bifurcate, long and numerous. Inner margin and line of concrescence coincide.

Remarks. Two subspecies of *C. purperi* are recognized: *C. purperi purperi* subsp. nov. having a broad, well-pronounced anterior marginal border and *C. purperi colombiaensis* subsp. nov. where there is a less well-pronounced marginal border, the surface pits extending to the valve edge.

C. purperi resembles both *C. locketti* (Stephenson 1935), described from the Miocene of Louisiana, and *C. salebrosa* Bold, 1963 from the Pliocene and Pleistocene of N. America and the Recent coasts of S. America (Sandberg 1964). *C. locketti* is distinguished by its strong postero-ventral flange tab on the right valve and the unique flange tab on the antero-ventral corner of the male dimorph. *C. salebrosa* has a very narrow anterior marginal zone, is distinctly convex in ventral outline, and is considerably wider in the posterior half when viewed dorsally. No noded forms of *C. purperi* have been found. *C. purperi* is placed in the genus *Cyprideis* rather than the allied genus *Cytheridea* on the absence of a vestibule, the ventral margin being incurved anterior of the mid-point (in *Cyprideis* the incurvature is in the posterior portion) and the generally more quadrate shape with pronounced sexual dimorphism. In *Cyprideis* the carapace is more strongly tapered to the posterior and dimorphism is not very pronounced. *C. purperi* resembles the genus *Heterocyprideis* Elofson, 1941 in the presence of anterior marginal teeth and a postero-ventral spine but unlike *Heterocyprideis* does not have an anterior vestibule, and is sulcate.

Cyprideis purperi purperi subsp. nov.

Plate 7, figs. 1–13; Plate 8, figs. 1, 2; text-fig. 2

1977 *Cytheridea* sp. nov. C Purper, pl. 3, figs. 1–4.
1977 *Cytheridea* sp. nov. D Purper, pl. 3, figs. 5–6.
?1977 *Cytheridea* sp. nov. E Purper, pl. 3, fig. 7.

Localities and horizon. Type locality, Pichua, Marañon River, Peru, from the Pebas Beds, Plio-Pleistocene. Other occurrences described by Purper 1977, from the Upper Amazon Basin, Brazil.

Material. Holotype, OS 10992, female right valve, and numerous valves and carapaces.

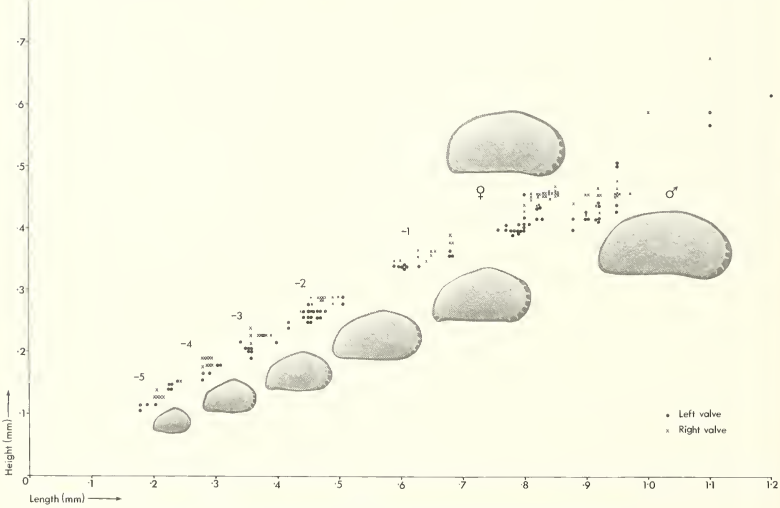
Dimensions

	L	H	W
Holotype:			
OS 10992 ♀ RV	0·81	0·44	
Paratypes:			
OS 10993 ♀ LV	0·83	0·44	
OS 10994 ♀ LV	0·84	0·45	
OS 10995 ♀ car.	0·84	0·45	0·40
OS 10996 ♀ car.	0·85	0·46	0·41
OS 10997 ♀ LV	0·85	0·46	
OS 10998 ♀ RV	0·83	0·43	
OS 10999 ♂ RV	0·97	0·46	
OS 11000 ♂ LV	0·97	0·48	
Paratypes:			
OS 11001 ♂ car.	0·95	0·46	0·40
OS 11002 ♂ RV	0·98	0·43	
OS 11004 juv. RV	0·24	0·16	
OS 11005 juv. RV	0·47	0·28	
OS 11006 juv. RV	0·63	0·35	
OS 11007 juv. RV	0·70	0·37	
OS 11008 ♂ p.m. RV	1·25	0·64	
OS 11009 ♀ p.m. LV	1·15	0·68	
OS 11010 juv. RV	0·37	0·23	

Diagnosis. Subspecies of *Cyprideis purperi* with relatively broad anterior marginal zone with pronounced smooth marginal groove.

Description. Subquadrate carapace ornamented with circular pits which cover valve surfaces apart from smooth anterior marginal zone. Hinge well-developed entomodont type which consists, in the left valve, of a posterior loculate socket with six to seven loculi, a median bar having a denticulate postero-median element, and a dentate antero-median element, and an anterior loculate socket with nine to ten loculi. Muscle scars: vertical row of four adductors, a V-shaped frontal scar, an oval mandibular scar, and a prominent fulcral point between the most dorsal adductor scar and the frontal scar. Marginal pore canals numerous and long, some bifurcate. Sexual dimorphism pronounced, females being shorter and more rounded posteriorly and wider in the posterior half than males.

Remarks: Text-fig. 2 shows an instar diagram of *C. purperi purperi* where an almost complete population of this subspecies is present in the Pichua sample, with five juvenile stages being represented. We found four specimens much larger in size than the normal adult but otherwise similar,



TEXT-FIG. 2. Instar diagram for *Cyprideis purperi purperi* subsp. nov.

although the anterior marginal spines are rather poorly developed. Purper (1977) figured a similar specimen as *Cytheridea* sp. nov. E. No juveniles are recognizable of this form. We propose that these large specimens are post-maturation moults of *Cyprideis purperi purperi.*

Cyprideis purperi colombiaensis subsp. nov.

Plate 8, figs. 3–9

Locality and horizon. Only from La Tagua, S. Colombia. Locality CAE/GEO/33, Plio-Pleistocene.

Material. Holotype, OS 11011, male left valve. Several single valves, mainly adult.

Dimensions. Holotype: OS 11011 ♂ LV L 0·80, H 0·40; Paratypes: OS 11003 ♂ RV L 0·88, H 0·42; OS 11012 ♂ RV L 0·88, H 0·40; OS 11013 ♂ RV L 0·90, H 0·42; OS 11014 ♀ RV L 0·79, H 0·42; OS 11015 ♀ LV L 0·79, H 0·42.

Diagnosis. Subspecies of *C. purperi* with surface ornamentation of subparallel rows of pits extending laterally to the free margins of the valves.

Description. The carapace is subquadrate in outline with a narrow anterior marginal border into which the ornamentation extends. All internal features are as for *C. purperi purperi* subsp. nov.

Remarks. C. purperi colombiaensis differs from *C. purperi purperi* by having a narrower anterior marginal border and having the ornamentation extended on to it; it is also somewhat thinner shelled. The duplicature is narrower and consequently the marginal pore canals are shorter, although in number and appearance are alike in the two subspecies. Juveniles indistinguishable.

Genus OTAROCYPRIDEIS gen. nov.

Derivation of name. Greek, *otos* meaning 'ear' referring to valve shape. Gender, feminine.

Type species. Otarocyprideis elegans sp. nov.

Diagnosis. A large, subrectangular ear-shaped genus of the Cytherideinae having rounded anterior margin and truncated posterior margin. Strong vestibules anteriorly and posteriorly; numerous dendritically branched marginal pore canals with ampullae. Marginal areas compressed. Hinge entomodont. Muscle scars with four vertically disposed adductors, heart-shaped frontal scar, oval mandibular scar, and pronounced fulcral point. Sexual dimorphism not obvious.

Remarks. The similarity of this genus to *Cyprideis* is obvious both in shape and hinge-type. Its generic status resides on the well-developed vestibules and the particularly well-branched dendritic marginal pore canals. *Cyprideis* has no vestibules and while the pore canals do exhibit branching the fine network of branches developed in *Otarocyprideis* is never seen in *Cyprideis.* The muscle scar pattern in the two genera is basically the same except that in *Cyprideis* the frontal scar is more open, obviously V-shaped and the position of the fulcral point is somewhat higher than in *Otarocyprideis.* Marginal teeth or spines are absent in this genus. Its close association with *Cyprideis* species suggests that this is a brackish water genus. *Otarocyprideis* is at present monotypic.

Otarocyprideis elegans sp. nov.

Plate 8, figs. 10–12; Plate 9, figs. 1–5, 7

1978 Ostracod B n.g.; n. sp. Purper, pl. 1, figs. 9–14.

Locality and horizon. Only from Pichua, Marañon River, Peru. Pebas Beds, Plio-Pleistocene.

Material. Holotype, OS 11028, right valve. Several additional valves and carapaces.

Dimensions

	L	H
Holotype:		
OS 11028 RV	1·07	0·48
Paratypes:		
OS 11029 LV	1·07	0·51
OS 11030 LV	1·00	0·51
OS 11031 RV	1·07	0·51

	L	H	W
Paratypes:			
OS 11032 car.	0·97	0·49	0·41
OS 11033 RV	0·79	0·36	
OS 11034 LV	0·97	0·48	
OS 11035 LV	1·00	0·49	
OS 11036 juv. RV	0·61	0·31	

Diagnosis. Smooth species of *Otarocyprideis* with broadly flattened anterior marginal area. Internal details as for genus.

Description. Carapace large (0·97–1·07 mm in length), smooth and featureless, apart from a shallow ridge along the anterior margin. Anterior margin broadly rounded, posterior obliquely truncate. Ventral margin broadly convex apart from just anterior to mid-point, where it is strongly incurved. Maximum height and length occurs medially. In dorsal view carapace parallel sided. Left valve larger than right, which it overlaps dorsally and overreaches anteriorly. Eye spots absent. In left valve hinge with posterior loculate socket, a denticulate median bar and an anterior loculate socket. Inner marginal areas very broad, with a well-developed vestibule anteriorly and a less prominent one posteriorly. Marginal pore canals numerous, long, and branch repeatedly, many of them having ampullae. Simple normal pore canals small, scattered evenly over the shell surface.

Juveniles of *O. elegans* are more quadrate with a more rounded posterior margin and straight ventral margin.

Remarks. O. elegans is quite distinct with respect to shape and dendritic marginal pore canals from all other species of cytherideid genera. It is common in the Pichua sample, with good preservation of adults and juveniles.

Genus BOTULOCYPRIDEIS gen. nov.

Derivation of name. Latin *botulus*, meaning 'sausage', referring to the carapace shape. Gender, feminine.

Type species. Botulocyprideis simplex sp. nov.

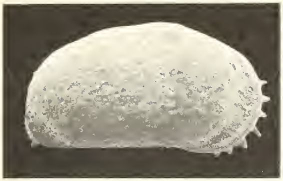
Diagnosis. Oval to subrectangular genus of Cytherideinae with rounded anterior and posterior margins. Hinge entomodont. Marginal pore canals short, numerous, some of which bifurcate. Inner margin and line of concrescence coincide. Non-dimorphic.

Remarks. This genus is distinguished from others of the Cytherideinae by its distinctive sausage-shaped carapace outline and the positive hinge elements occurring in the left valve. *Eucytheridea* Bronstein (see Bold 1961) has a similar external appearance to *Botulocyprideis* but differs internally by the possession of a large anterior vestibule and simple marginal pore canals. *Neocyprideis* Apostolescu, 1956 grows to a larger size, is more subrectangular in shape due to the pronounced posterior cardinal angle, and tends to have a more strongly developed hinge, with narrower duplicature than *Botulocyprideis*.

EXPLANATION OF PLATE 7

Figs. 1–13. *Cyprideis purperi purperi* subsp. nov., Pebas Beds, Peru. 1, external view, female right valve, holotype, OS 10992, ×62. 2, 6, internal view, female left valve, ×62, and muscle scars, ×169. 3, dorsal view to show hinge teeth, female right valve, paratype, OS 10998, ×98. 4, anterior marginal pore canals, by transmitted light, seen from the inside, male right valve, paratype, OS 11002, ×292. 5, external view, female left valve, paratype, OS 10997, ×62. 7, dorsal view, female carapace, paratype, OS 10996, ×65. 8, ventral view, female carapace, paratype, OS 10995, ×64. 9, external view, male right valve, paratype, OS 10999, ×63. 10, external view, male left valve, paratype, OS 11000, ×62. 11, external view, juv. right valve, paratype, OS 11005, ×62. 12, external view, right valve, post-maturation moult, male paratype, OS 11008, ×48. 13, external view, left valve, post-maturation moult, female paratype, OS 11009, ×48.

PLATE 7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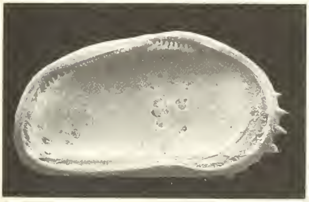
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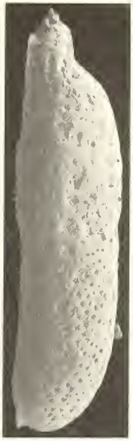
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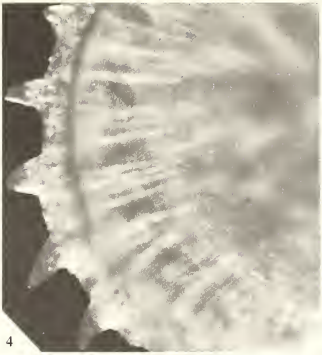
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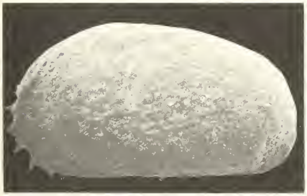
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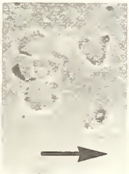
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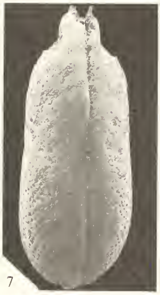
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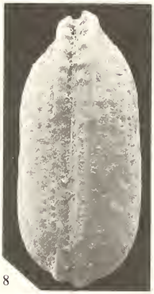
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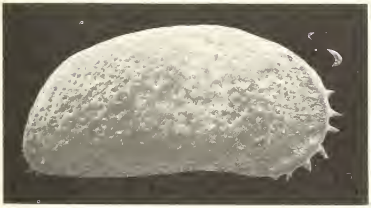
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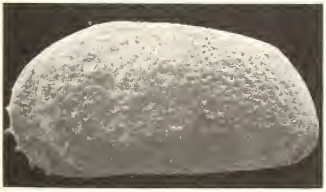
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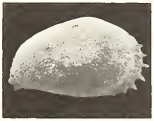
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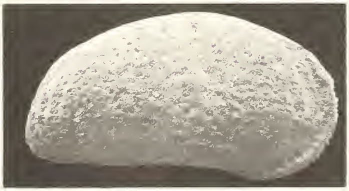
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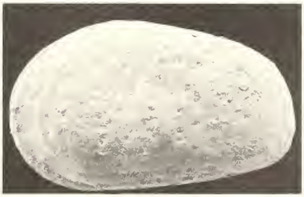
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SHEPPARD and BATE, *Cyprideis*

Botulocyprideis simplex sp. nov.

Plate 9, figs. 6, 8–13

Locality and horizon. Only from Pichua, Marañon River, Peru. Pebas Beds, Plio-Pleistocene.

Material. Holotype, OS 11077, right valve. A few additional single valves.

Dimensions. Holotype: L 0·61, H 0·29; Paratypes: OS 11078 RV L 0·61, H 0·31; OS 11079 LV L 0·60, H 0·28; OS 11080 RV L 0·61, H 0·29; OS 11081 LV L 0·61, H 0·29; OS 11082 LV L 0·62, H 0·30.

Diagnosis. Smooth species of *Botulocyprideis* with parallel dorsal and ventral margins and well-rounded anterior and posterior margins. Hinge is a reversed version of *Cyprideis*-type with positive terminal elements in left valve. Inner margin and line of concrescence coincide.

Description. Carapace ovoid with straight, parallel dorsal and ventral margins, parallel-sided in dorsal view. Greatest length and height both pass through mid-point. Valve surface completely smooth and featureless. Internally, marginal areas of moderate width; marginal pore canals numerous, evenly spaced with some bifurcating. Hinge weakly developed and consists, in the left valve, of an elongated anterior dentate tooth, a median locellate groove, and a short posterior dentate tooth. Muscle scars of *Cyprideis*-type, with vertical row of four equal-sized oval adductors, oval frontal scar which is slightly indented at the top giving a heart-shaped appearance, oval mandibular scar, and a pronounced fulcral point.

Remarks. B. simplex resembles Ostracod A.n.g., n. sp. (Purper 1977) from the Tertiary of Brazil but differs chiefly on marginal pore canals. Those of Purper's species are long and branch many times, and from her illustrations there appears to be a vestibule anteriorly at least. *Eucytheridea bradii* (Norman, 1865) (see Bold 1961, p. 287) has a similar though not identical external appearance and internally differs by the possession of a well-developed anterior vestibule. *B. simplex* may be confused with the juveniles of *O. elegans* as they are about the same size and shape, from the same locality. The inner marginal area in *O. elegans* is much wider, vestibules are developed, and the positive terminal hinge elements occur in the right valve rather than the left. *Neocyprideis parallela* (Lienenklaus, 1905) an Oligocene form as figured by Malz (1973*a*) is similar in outline but is somewhat larger (length about 0·75 mm) with laterally compressed anterior, posterior, and ventral margins, and short, widely spaced simple marginal pore canals.

Family ILYOCYPRIDIDAE Kaufmann, 1900
Subfamily ILYOCYPRIDINAE Kaufmann, 1900
Genus PELOCYPRIS Klie, 1939
Pelocypris zilchi Triebel, 1953

Plate 10, figs. 8–13; text-fig. 3

1953 *Pelocypris zilchi* n. sp.; E. Triebel, p. 2, pl. 1, figs. 1–8.

Type locality and horizon. Barranca El Sisimico, about 15 km north-east of Vulkan San Vicente (El Salvador). Pleistocene.

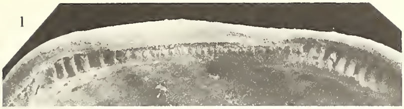
EXPLANATION OF PLATE 8

Figs. 1, 2. *Cyprideis purperi purperi* subsp. nov., Pebas Beds, Peru. 1, hinge, left valve, female paratype, OS 10993, ×152. 2, hinge, right valve, female holotype, OS 10992, ×145.

Figs. 3–9. *Cyprideis purperi colombiaensis* subsp. nov., locality CAE/GEO/33, Colombia. 3, 8, 9, external and internal view, male left valve, ×62, and sieve plate, ×2K, holotype, OS 11011. 4, 6, 7, external and internal views, ×62, and muscle scars, ×500, male right valve, paratype, OS 11012. 5, anterior marginal pore canals, by transmitted light, seen from the inside, male right valve, paratype, OS 11003, ×209.

Figs. 10–12. *Otarocyprideis elegans* gen. et sp. nov., Pebas Beds, Peru. 10, branching anterior marginal pore canals, by transmitted light, seen from the inside, left valve, paratype, OS 11035, ×198. 11, muscle scars, right valve, paratype, OS 11033, ×500. 12, dorsal view, carapace, paratype, OS 11032, ×51.

PLATE 8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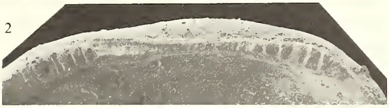
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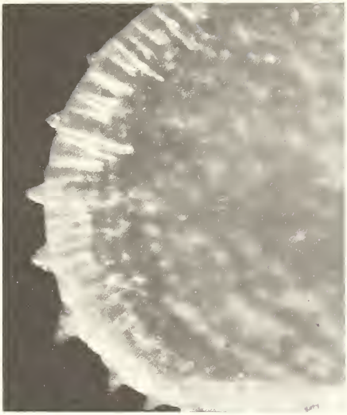
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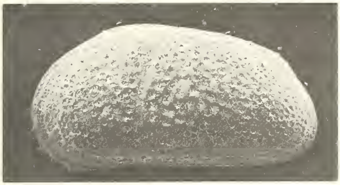
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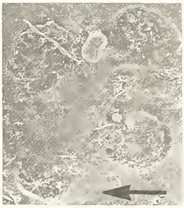
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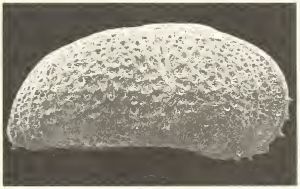
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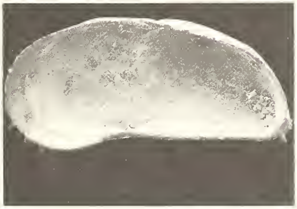
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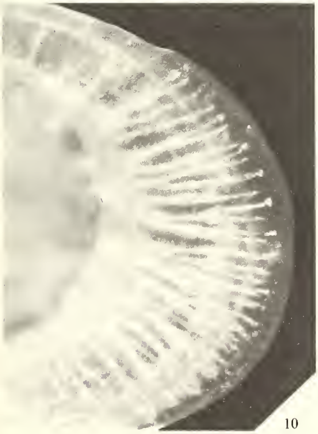
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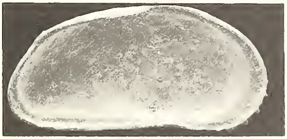
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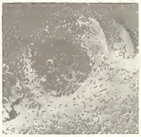
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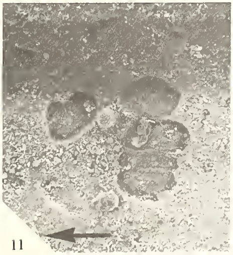
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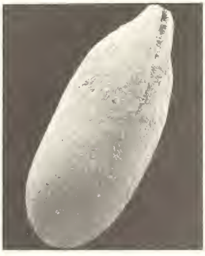
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SHEPPARD and BATE, Plio-Pleistocene ostracods

New material. A few adult and juvenile valves only from locality CAE/GEO/33, La Tagua, S. Colombia.

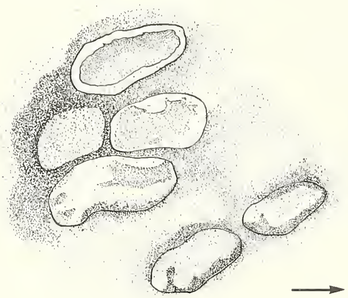
Dimensions. OS 11066 LV L 1·33, H 0·82; OS 11067 RV L 1·18, H 0·64; OS 11068 RV L 1·05, H 0·60; OS 11069 LV L 0·60, H 0·32.

Diagnosis. Bisulcate species of *Pelocypris* with pitted shell surface and dentate valve margin in right valve only.

Description. Carapace is subquadrate in shape with high anterior shoulder from which extend two short dorsomedian sulci. Anterior and posterior margins are broadly rounded; ventral margin almost straight, dorsal margin is sinuous. Greatest height of shell occurs anterior to mid-point, greatest width is in posterior half. Surface ornamentation of rounded pits which decrease in size towards valve edges; small tubercles around anterior and posterior margins. Entire valve margin in right valve evenly dentate (Pl. 10, figs. 10, 12) whereas that of left valve is smooth. Duplicature narrow. Narrow vestibules are developed anteriorly and posteriorly. Marginal pore canals have not been observed. Muscle scars consist of a subvertical row of three irregularly sized oval adductors situated on a vertical ridge which corresponds to the position of the external sulci. Behind the adductor scars, situated in a depression, a rather inconspicuous scar may be observed. Two elongate (mandibular?) scars are situated below and to the front of this group of scars (text-fig. 3). The hinge is of a simple adont form.

Remarks. The juveniles of *P. zilchi* differ markedly from the adult specimens by being distinctly ovoid with maximum width medially, and by lacking the sulci and associated high flattened shoulder. The ornamentation and internal features are, however, recognizable. The diagnostic dentate right valve margin and the marginal tubercles do not appear to be developed until the adult stage. A species which is geographically not very far removed from this Colombian species is *P. lenzi* Klie, 1939*b*, a Recent form from Brazil, but this has eight or nine long heavy spines on the anterior and posterior borders of both valves.

Species of *Pelocypris* are considered to inhabit fresh water environments.

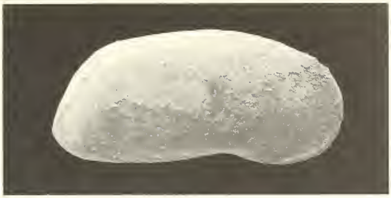


TEXT-FIG. 3. Muscle scars of *Pelocypris zilchi* Triebel, left valve, OS 11066 ×605.

EXPLANATION OF PLATE 9

Figs. 1–5, 7. *Otarocyprideis elegans* gen. et sp. nov., Pebas Beds, Peru. 1, external view, right valve, holotype, OS 11028, ×51. 2, internal view, right valve, paratype, OS 11031, ×51. 3, external view, left valve, paratype, OS 11029, ×51. 4, 5, internal view, ×51, and hinge, ×100, left valve, paratype, OS 11034. 7, external view, juvenile right valve, paratype, OS 11036, ×51.

Figs. 6, 8–13. *Botulocyprideis simplex* gen. et sp. nov., Pebas Beds, Peru. 6, external view, right valve, holotype, OS 11077, ×76. 8, 10, 12, muscle scars, ×500, internal view, ×76, hinge, ×200, left valve, paratype, OS 11079. 9, 11, internal view, ×76, hinge, ×200, right valve, paratype, OS 11078. 13, anterior marginal pore canals, ×180, right valve, paratype, OS 11080.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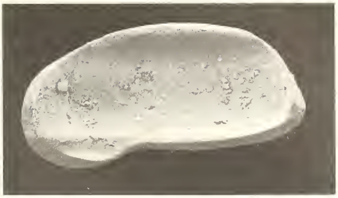
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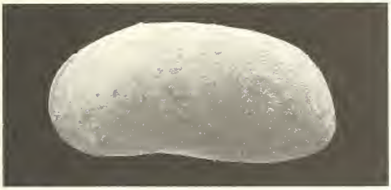
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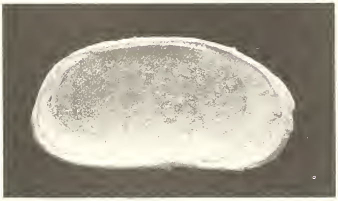
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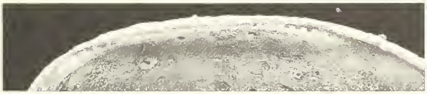
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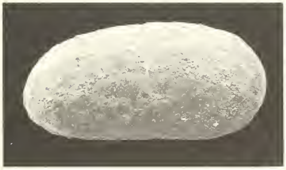
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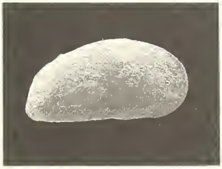
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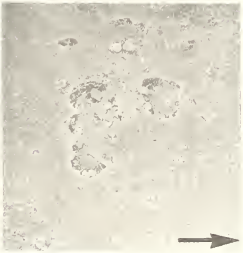
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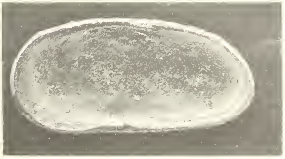
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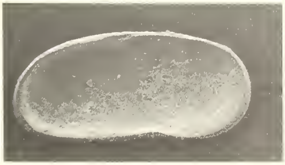
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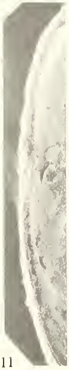
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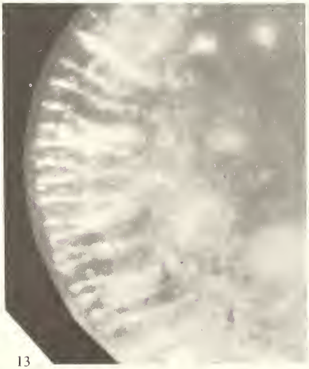
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SHEPPARD and BATE, Plio-Pleistocene ostracods

Pelocypris sp.

Plate 10, fig. 14

Remarks. One broken specimen (OS 11071) of a noded species of *Pelocypris* was found in sample CAE/GEO/33. It is left under open nomenclature.

Family LIMNOCYTHERIDAE Klie, 1938

Genus CYTHERIDELLA Daday, 1905

Cytheridella postornata sp. nov.

Plate 10, figs. 1–7

Derivation of name. From the Latin, ornamented posterior.

Locality and horizon. Type locality, La Tagua, S. Colombia. Locality CAE/GEO/54, Plio-Pleistocene, and locality CAE/GEO/33, Colombia.

Material. Holotype, OS 11072, left valve. Two adult valves and several juvenile valves from locality CAE/GEO/54.

Dimensions. Holotype: OS 11072 LV L 1·10, H 0·60; Paratypes: OS 11073 RV L 1·08, H 0·60; OS 11074 juv. LV L 0·62, H 0·34; OS 11075 juv. LV L 0·68, H 0·38; OS 11076 broken LV, H 0·50.

Diagnosis. Species of *Cytheridella* with deep dorso-median sulcus dividing carapace into smooth anterior portion and swollen pitted posterior. Broad, compressed, anterior margin.

Description. Dorsal and ventral margins of carapace parallel, anterior and posterior broadly rounded. Posterior half greatly swollen and postero-ventral portion overhangs ventral margin so that carapace is an inverted heart-shape when viewed dorsally. Ornamentation of small circular pits on posterior half only. Deep dorso-median sulcus extends about two-thirds of the way down the valves. Smooth anterior margin broad and compressed. Hinge a simple adont development where selvage of right valve fits into flange groove of left valve. Selvage developed equally round valve margins. Duplicature narrow and there is a narrow posterior vestibule. Muscle scars consist of a vertical row of four adductors on a ridge corresponding to the outside sulcus dividing the carapace into two parts (see Pl. 10, figs. 4, 5).

Remarks. Cytheridella species are strongly dimorphic. The two adult specimens observed in sample CAE/GEO/54 are considered females because of the pronounced posterior swelling. *C. postornata* sp. nov. is most similar to living species of the genus. It resembles the type species *C. ilosvayi* Daday, 1905 (see Purper 1974) and *C. boldi* Purper, 1974, both from S. America. *C. ilosvayi* is not so strongly sulcate as *C. postornata* externally, has pits over the entire shell surface, a rather sinuous dorsal margin, and the anterior margin is somewhat narrower. Internally the major difference between the two species lies in the well-developed anterior vestibule in *C. ilosvayi*. *C. boldi* is also pitted over the entire shell surface. The female dimorph of *C. boldi* is not so strongly swollen posteriorly as *C. postornata*, and the ventro-lateral part of the shell does not overhang the ventral

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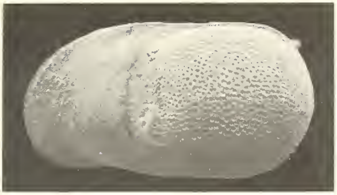
EXPLANATION OF PLATE 10

Figs. 1–7. *Cytheridella postornata* sp. nov., locality CAE/GEO/54, Colombia. 1, 2, 4, 6, left valve, holotype, OS 11072. 1, external view, ×51. 2, hinge, ×100. 4, muscle scars, ×1K. 6, internal view, ×51. 3, 5, 7, external and internal views, right valve, paratype, OS 11073, ×51. 5, muscle scars, ×1K.

Figs. 8–13. *Pelocypris zilchi* Triebel, 1953, locality CAE/GEO/33, Colombia. 8, 9, external and internal views, left valve, OS 11066, ×42. 10, duplicature, and dentate anterior shell margin, right valve, OS 11068, ×71. 11, juv. left valve, OS 11069, ×42. 12, 13, enlarged anterior margin, ×71, and external view, ×42, right valve, OS 11067.

Fig. 14. *Pelocypris* sp., locality CAE/GEO/33, Colombia, broken fragment of right valve showing development of surface nodes, OS 11071, ×42.

PLATE 10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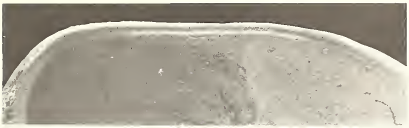
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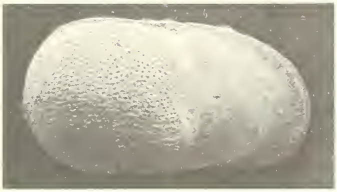
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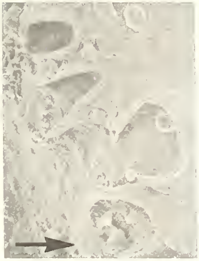
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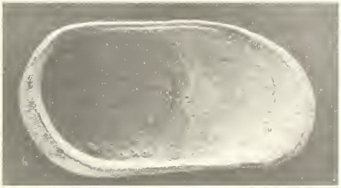
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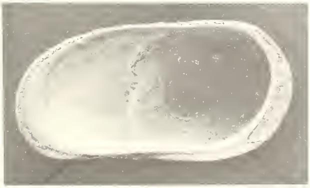
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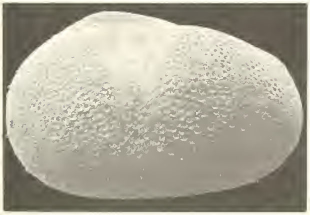
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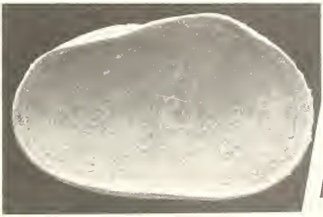
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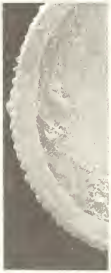
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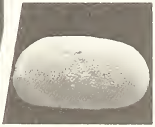
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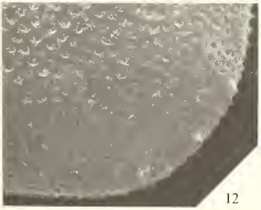
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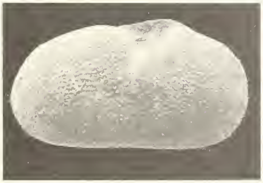
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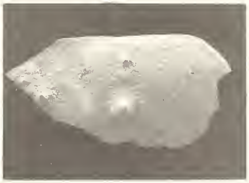
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SHEPPARD and BATE, Plio-Pleistocene ostracods

margin so far. *C. monodi* Klie, 1936, another Recent species, differs from *C. postornata* in having its greatest width in the median part of the carapace and tapering posteriorly. The Eocene species *C. strangulata* (Jones, 1860) is obliquely rounded anteriorly, irregularly ovoid in dorsal view, and triangular in posterior view.

Family CYTHERIDAE Baird, 1850
Subfamily TRACHYLEBERIDINAE Sylvester-Bradley, 1948
Genus AMBOCYTHERE Bold, 1958
Ambocythere campana sp. nov.

Plate 11, figs. 1–9

Derivation of name. Latin, bell, referring to the shape of the posterior.

Locality and horizon. Only from La Tagua, S. Colombia, locality CAE/GEO/33. Plio-Pleistocene. Known only from the type locality and horizon.

Material. Holotype, OS 11037, female carapace. Several additional single valves and carapaces.

Dimensions

	L	H	W
Holotype:			
OS 11037 ♀ car.	0·54	0·34	0·29
Paratypes:			
OS 11038 ♀ car.	0·57	0·34	0·26
OS 11039 ♂ RV	0·63	0·33	
OS 11040 ♂ LV	0·61	0·34	

	L	H
Paratypes:		
OS 11041 ♀ LV	0·60	0·34
OS 11042 juv. LV	0·47	0·26
OS 11043 broken ♀ LV	0·48	—
OS 11045 juv. LV	0·37	0·24
OS 11046 juv. LV	0·47	0·29

Diagnosis. Species of *Ambocythere* with reticulate ornamentation and bell-shaped posterior margin.

Description. Carapace pyriform to subquadrate in lateral view with greatest height in anterior third passing through anterior cardinal angle, and greatest length medially. Anterior margin broadly rounded, with strong carina-like rim parallel to it and extending dorsally to mid-point of dorsal margin and ventrally to about two-thirds along ventral margin. Dorsal margin short, straight, and slopes steeply just before the posterior cardinal angle where it becomes strongly incurved, giving the bell-end appearance to the obliquely truncate posterior. Carapace widest posteriorly. Left valve slightly larger than right, which it overlaps dorsally in the central part of dorsal margin.

Shell surface covered with reticulation of irregularly shaped pits which develop into several shallow lateral ridges, extending on to ventro-lateral and ventral surfaces, some of which curve up and follow the posterior margin. Near anterior marginal area, just behind marginal rim, the pits decrease in size and become arranged in parallel rows. These pits are also present in front of the rim, right up to the valve edge. Hinge-line straight. In left valve hinge consists of a deep anterior socket with a postadjacent knob-like process, which curves round beneath the socket, forming an anterior expansion of the median bar. Median bar itself is narrow and smooth and terminates just prior to the posterior smooth socket. It is the up-turning of the dorsal margin in the

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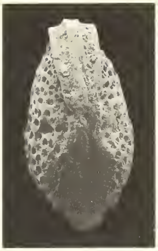
EXPLANATION OF PLATE 11

Figs. 1–9. *Ambocythere campana* sp. nov., locality CAE/GEO/33, Colombia. 1, 6, female carapace, holotype, OS 11037, dorsal and ventral views, × 76 and × 103. 2, right side, female carapace, paratype, OS 11038, × 83. 3, right valve, male paratype, OS 11039, × 83. 4, juv. left valve, paratype, OS 11046, × 85. 5, male left valve, paratype, OS 11040, × 83. 7, juv. left valve, paratype, OS 11045, × 83. 8, 9, internal view, × 83, and hinge, × 143, female left valve, paratype, OS 11041.

Figs. 10–16. *Rhadinocytherura amazonensis* gen. et sp. nov. 10, 16, right valve, holotype, OS 11047, locality CAE/GEO/33, Colombia. 10, external view, × 150. 16, enlargement of surface pitting, × 1K. 11, 13, left valve, paratype, OS 11052, locality CAE/GEO/33, Colombia. 11, external view, × 150. 13, enlargement of hinge, × 288. 12, 14, right valve, paratype, OS 11048, Pebas Beds, Peru. 12, internal view, × 150. 14, hinge, × 288. 15, dorsal view, carapace, paratype, OS 11050, Pebas Beds, Peru, × 150.

PLATE 11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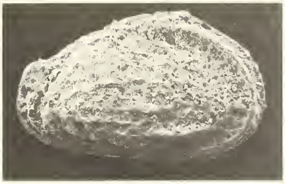
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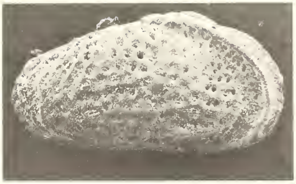
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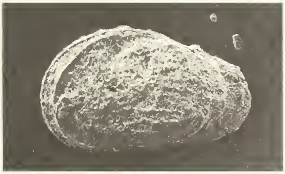
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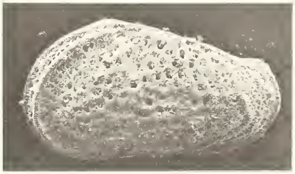
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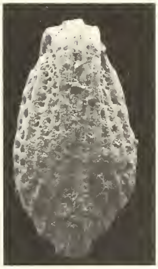
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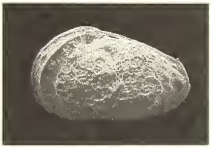
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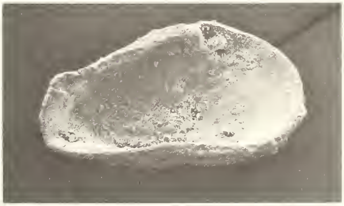
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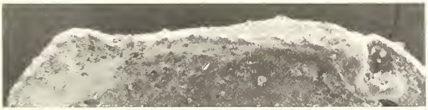
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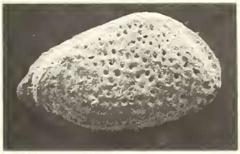
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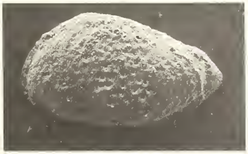
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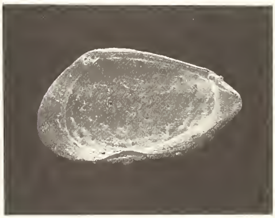
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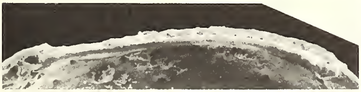
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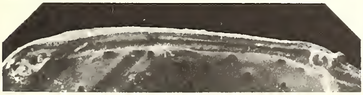
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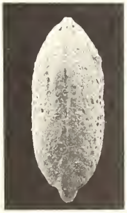
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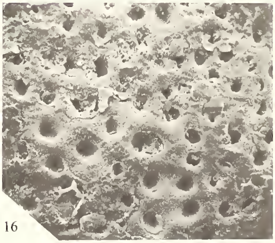
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SHEPPARD and BATE, Plio-Pleistocene ostracods

region of the posterior cardinal angle which accommodates this posterior socket. Internally marginal area very broad anteriorly; inner margin and line of concrescence coincide; marginal pore canals long, numerous, and evenly spaced. Muscle scars not seen. Sexual dimorphism pronounced, females shorter and rather subquadrate, males more triangular laterally.

Remarks. This species has been placed in the genus *Ambocythere* despite lacking the usual denticulate, laterally projecting flange on the postero-ventral margin. Two morphologically similar genera are *Munseyella* Bold, 1957, and *Phacorhabdotus* Howe and Laurencich, 1958. Characteristic features of *Munseyella* include few marginal pore canals, the presence of vestibules anteriorly and posteriorly, and generally quadrate shape. None of these are shown on our material. *Phacorhabdotus* typically has subcentral tubercles on both valves, an eye node and prominent lateral ridges, broad compressed posterior and anterior marginal areas, and a holamphidont hinge.

Of the described *Ambocythere* species the closest to *A. campana* is *A. bodjonegoroensis* (Kingma, 1948) from the Pliocene of Java. The reticulate ornamentation here is very similar but the anterior marginal zone either side of the marginal rim is smooth. The dorsal margin slopes very steeply to the posterior which is much more obliquely truncate than in *A. campana*. A species which is possibly more closely allied to the present species has been described as *A.* aff. *bodjonegoroensis* Bold, 1965, a Miocene form from Trinidad and Venezuela where the reticulation extends further forward and the dorsal margin slopes less strongly to the posterior. *A. campana* is, however, distinguishable from both these species by its distinctly shaped posterior margin and the presence of the lateral ridges. All other described species of *Ambocythere* have surface ornamentation of ridges in various number and arrangement.

Family CYTHERURIDAE Müller, 1894

Genus RHADINOCYTHERURA gen. nov.

Derivation of name. Latin *Rhadinos*, slender + *Cytherura*. Gender, feminine.

Type species. *Rhadinocytherura amazonensis* sp. nov.

Diagnosis. A subovate to subquadrate genus of the Cytheruridae; rounded anterior and small triangular posterior with caudal process; smooth eye swelling. Well-developed vestibules at anterior and posterior ends. Hinge is modified peratodont with anterior terminal element lacking.

Remarks. The hinge of *Rhadinocytherura* is quite unique, being essentially peratodont in which the expansion of the median element is more pronounced anteriorly and where the anterior terminal element is absent in both valves. The hinge therefore comprises, in the left valve, a posterior loculate socket, a smooth median bar which expands slightly postero-medially and which is developed into a dentate anterior tooth. There is no anterior socket. An accommodation groove is present. The corresponding elements in the right valve are a posterior dentate tooth with an adjacent deep postero-median groove which narrows anteriorly where it is connected to a deeper loculate socket. Both the posterior terminal element and the antero-median element are divided into three parts. Text-fig. 4 shows the difference between the hinge of *Rhadinocytherura* and that of *Semicytherura* which has a typical Peratodont type hinge.

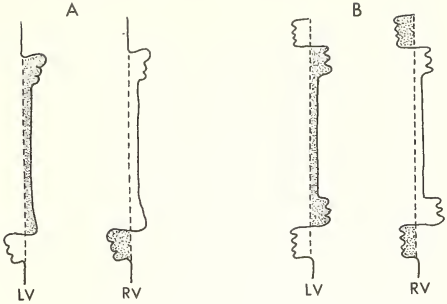
The carapace shape, size, and the presence of a caudal process place this genus into the Cytheruridae. The hinge, however, is obviously different and it may be necessary at a later date to erect a different taxonomic group based solely on this feature.

Rhadinocytherura amazonensis sp. nov.

Plate 11, figs. 10–16

Locality and horizon. Type locality, La Tagua, S. Colombia, locality CAE/GEO/33, Plio-Pleistocene; also from the Pebas Beds at Pichua, Marañon River, Peru.

Material. Holotype, OS 11047, RV, from locality CAE/GEO/33; several additional valves and carapaces.



TEXT-FIG. 4. Diagrammatic reconstruction of *Rhadinocytherura* hinge (A) in comparison with typical Peratodont hinge as in *Semicytherura* (B).

Dimensions

	L	H	W
Holotype:			
OS 11047 RV	0·26	0·15	
Paratypes:			
OS 11048 RV	0·26	0·15	
OS 11049 RV	0·26	0·15	

	L	H	W
Paratypes:			
OS 11050 car.	0·24	0·13	0·09
OS 11052 LV	0·26	0·15	
OS 11053 LV	0·27	0·15	
OS 11054 RV	0·25	0·15	

Diagnosis. Species of *Rhadinocytherura* with surface ornamentation of subcircular pits.

Description. Carapace small (0·24–0·26 mm in length), subovate to subquadrate, highest anteriorly and with greatest length medially. Dorsal margin strongly arched with apex at anterior cardinal angle; ventral margin convex. Anterior broadly rounded and slightly compressed at extreme valve edges; posterior triangular, with distinct caudal process. Posterior margin broadly flattened and extends ventrally for about one-third of ventral margin. In dorsal view the valves are perfectly parallel-sided. Surface with small subcircular pits arranged roughly in rows parallel to ventral margin and bend up to follow the anterior and posterior margins. The slight eye swelling in the region of the anterior cardinal angle is smooth; so too is the compressed postero-ventral border. Pore canals simple, irregularly scattered over the shell surface. Inner marginal areas are broad with well-developed vestibules both anteriorly and posteriorly. Muscle scars consist of a vertical row of four connected adductor scars of unequal size; the frontal scar has not been observed. The hinge has already been discussed in detail for the genus. Sexual dimorphism has not been observed in this species.

Remarks. Ostracod D n.g., n. sp. Purper, 1977, is very close to *R. amazonensis* in valve outline, ornamentation, and presence of a caudal process and an eye swelling. The muscle scars, however, consist of four separate vertical adductors, an elongate frontal scar, and a distinct mandibular scar. The figured hinge shows a weakly denticulate median bar which is swollen more or less equally at both ends; this is clearly distinguishable from that of *R. amazonensis*. There is no other record of any similar species.

R. amazonensis is considered a marine to brackish-water form.

Family CYTHERIDAE Baird, 1850
Subfamily PERISSOCYTHERIDEINAE Bold, 1963
Genus PERISSOCYTHERIDEA Stephenson, 1938
Perissocytheridea formosa sp. nov.

Plate 12, figs. 1–6, 8, 10–12

Derivation of name. Latin, *formosus*, beautifully formed, referring to the surface ornamentation.

Locality and horizon. Only from La Tagua, S. Colombia, locality CAE/GEO/33, Plio-Pleistocene.

Material. Holotype, OS 11056, female right valve, and several single valves.

Dimensions

Holotype:	L	H	W
OS 11056 ♀ RV	0·36	0·23	
Paratypes:			
OS 11044 ♀ car.	0·35	0·19	0·17
OS 11051 ♀ RV	0·36	0·21	
OS 11057 ♀ LV	0·35	0·20	

Paratypes:	L	H
OS 11058 ♀ LV	0·36	0·21
OS 11059 ♂ RV	0·40	0·21
OS 11060 ♀ RV	0·37	0·21
OS 11061 ♂ RV	0·38	0·21

Diagnosis. Species of *Perissocytheridea* with heavily sculptured pitted shell surface and strong ventro-lateral alar development.

Description. Carapace small (0·35–0·40 mm in length), subpyriform to subquadrate in lateral view with nearly straight dorsal margin and convex ventral margin. Left valve the larger: anterior broadly rounded, posterior triangular. Anterior and posterior cardinal angles well defined; a shallow sulcus extends down from the region of the anterior cardinal angle to approximately the mid-point of each valve. Extension of the shell developed ventro-laterally into a ridge which is definitely wing-like in some specimens. The greatest height, equal to about half the length, is in the anterior third, passing through the anterior cardinal angle; greatest length passes through mid-point of the shell. Surface ornamentation of irregularly shaped and arranged deep pits, forming parallel rows around the anterior margin. Anterior border compressed, so too to a lesser extent is the postero-ventral border. Sexual dimorphism pronounced, females shorter, taller, and more subquadrate. The dorsal margin in the males has a tendency to become slightly incurved towards the posterior. Normal pore canals large, with sieve-plates, few in number and scattered evenly over the shell. Internally the hinge is a weakly developed antimerodont type with, in the left valve, terminal loculate sockets connected by an intervening denticulate median bar. The inner margin and line of concrescence apparently coincide; duplicature narrow. Muscle scars not seen.

Remarks. The juveniles of *P. formosa* have weakly developed ornamentation but strongly developed wing-like processes.

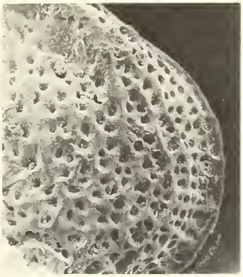
The type species of *Perissocytheridea*, *P. matsoni* (Stephenson, 1935), a Miocene species from Louisiana, U.S.A., closely resembles *P. formosa* in ornamentation but differs by being more strongly sulcate, by tapering more to the posterior, and by being more inflated postero-dorsally in the male dimorph. *P. formosa* is not similar to living species of *Perissocytheridea*. *P. gibba* (Klie, 1939*a*), originally described from Brazil, is a non-sulcate, smooth-shelled species with broadly compressed marginal areas both posteriorly and anteriorly. *P. krömmelbeini* Pinto and Ornellas, 1970 described from a brackish-water lagoon channel from Southern Brazil, is a strongly pitted species, like *P. formosa*, but differs by possessing a distinct swelling to the carapace in the postero-dorsal and antero-median regions. *P. meyerabichi* (Hartmann) (see Swain 1967), described from the Gulf of California, is distinguished by its coarsely reticulate surface ornamentation. Van den Bold (1975) described a species as *Perissocytheridea* sp. B from the Pliocene of the Dominican Republic which is close to *P. formosa* in shape and ornament. It is distinguished from *P. formosa* by possessing a horizontal sulcus which runs from the valve centre to the posterior margin. It is noted that *P. formosa* does not possess the terminal vestibules which are characteristic of the genus. We do, however, consider that the shape, sulcation, ornament, and hinge adequately ally this species to *Perissocytheridea*.

EXPLANATION OF PLATE 12

Figs. 1–6, 8, 10–12. *Perissocytheridea formosa* sp. nov., locality CAE/GEO/33, Colombia. 1–3, 8, 12, female right valve, holotype, OS 11056. 1, anterior enlarged to show ornamentation, ×248. 2, 3, external and internal views, ×111. 8, enlarged view of hinge, ×222. 12, sieve plate, ×5K. 4, 6, female left valve, paratype, OS 11057, external view, ×111, and hinge, ×222. 5, left side, female carapace, paratype, OS 11044, ×111. 10, male left valve (specimen lost), ×111. 11, male right valve, paratype, OS 11059, ×111.

Figs. 7, 9, 13–18. *Perissocytheridea*? *elongata* sp. nov., Pebas Beds, Peru. 7, 16, 17, left valve, paratype, OS 11064. 7, hinge, ×222. 16, internal view, ×111. 17, muscle scars, ×2K. 9, 15, right valve, paratype, OS 11063, hinge, ×222, internal view, ×111. 13, external view, right valve, holotype, OS 11062, ×111. 14, 18, external views, left valve, paratype, OS 11065, (14) ×111, (18) ×172.

PLATE 12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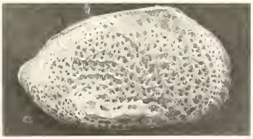
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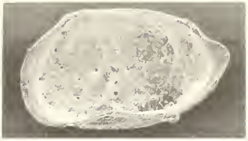
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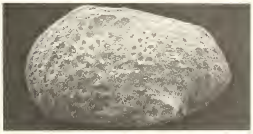
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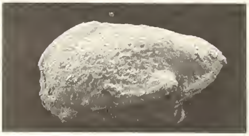
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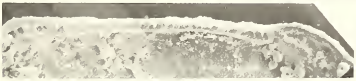
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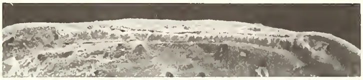
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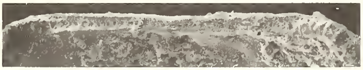
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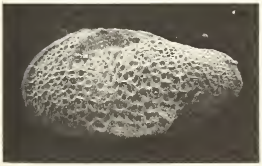
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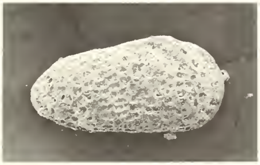
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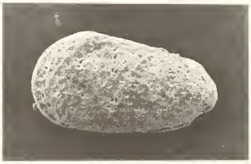
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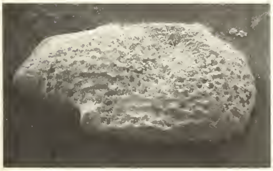
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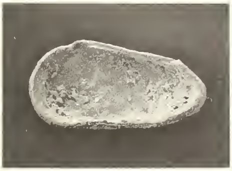
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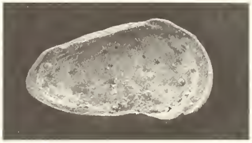
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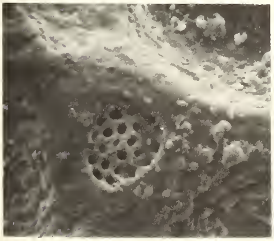
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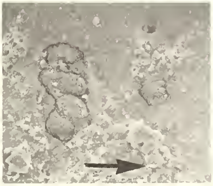
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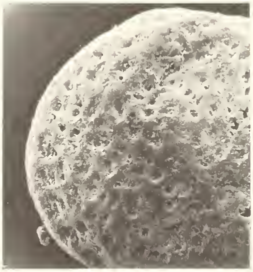
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SHEPPARD and BATE, Plio-Pleistocene ostracods

Perissocytheridea? *elongata* sp. nov.

Plate 12, figs. 7, 9, 13–18

Locality and horizon. Only from Pichua, Marañon River, Peru. Pebas Beds, Plio-Pleistocene.

Material. Holotype, OS 11062, right valve. Three paratypes.

Dimensions. Holotype: OS 11062 RV L 0·33, H 0·17; Paratypes: OS 11063 RV L 0·30, H 0·17; OS 11064 LV L 0·31, H 0·17; OS 11065 LV L 0·32, H 0·18.

Diagnosis. Elongate species of *Perissocytheridea*? with pitted shell surface and weakly developed alae.

Description. Carapace small (0·30–0·33 mm in length), elongate, subrectangular to triangular, greatest height occurring in the anterior third, greatest length passing below mid-point. Dorsal margin straight, ventral margin straight to slightly convex. Anterior margin broadly rounded and compressed: posterior is triangular due to the tapering postero-dorsal and postero-ventral slopes. Carapace much compressed in dorsal view, valves more or less parallel sided; the greatest width occurs medially. On each valve there is a slight lateral swelling of the shell in a postero-ventral position; this alate development is more pronounced in some specimens than in others. Surface ornamentation of small irregularly shaped pits which, around the anterior border, develop into a single row of large evenly spaced depressions. Shallow sulcus present in an antero-dorsal position which describes a small arc following the anterior margin for about a third of its distance. Normal pore canals large, apparently simple, and scattered widely over the shell surface.

Internally hinge straight, well developed, of antimerodont type with, in the left valve, an anterior loculate socket, a median denticulate bar, and a posterior loculate socket. There is a tendency for the median bar to become more coarsely dentate at the extreme anterior and posterior ends. Correspondingly, in the right valve the hinge elements consist of terminal teeth separated by a locellate median groove. Muscle scars a vertical row of four oval adductors. The only frontal scar which has been observed is apparently oval but this is somewhat obscured. Duplicature narrow, inner margin and line of concrescence coinciding throughout; marginal pore canals not seen. Sexual dimorphism is not apparent.

Remarks. In 1977 Purper figured a species from the late Tertiary of Brazil which she named *Perissocytheridea* sp. nov. A. Apart from being rather more sulcate, this very closely resembles *P.*? *elongata* but from the illustrations alone, with no description, it would be unreasonable to place this in synonymy with the present species.

P.? *elongata* is distinct from any described species of the genus. Because of the lack of obvious sexual dimorphism, absence of vestibules, and elongate shape this species is not a typical *Perissocytheridea*. The ornament, hinge, and sulcation (although not pronounced) are otherwise characteristic of the genus, to which it is tentatively assigned.

Superfamily CYPRIDACEA Baird, 1846
Family CYCLOCYPRIDIDAE Kaufmann, 1900
Genus CYPRIA Zenker, 1854
Cypria aqualica sp. nov.

Plate 13, figs. 1–6

Derivation of name. Latin, *aqualicus*, belly, referring to the rotund shape of the shell.

Locality and horizon. Type locality Pichua, Marañon River, Peru, from the Pebas Beds, Plio-Pleistocene. Also locality CAE/GEO/33, La Tagua, S. Colombia.

Material. Holotype, OS 11016, left valve. A few single valves and one broken carapace.

Dimensions

	L	H
Holotype:		
OS 11016 LV	0·61	0·43
Paratypes:		
OS 11017 RV	0·60	0·42
OS 11018 broken LV	—	—

	L	H	W
Paratypes:			
OS 11019 broken car.	0·59	—	0·24
OS 11020 juv. LV	0·32	0·24	
OS 11021 LV	0·49	0·36	
OS 11022 RV	0·53	0·38	

Diagnosis. Smooth-shelled species of *Cypria* with broadly rounded anterior and posterior margins, straight to slightly concave ventral margin, and convex dorsal outline with pronounced posterior cardinal angle.

Description. Thin-shelled fragile carapace, subovate, with greatest height and length occurring medially. Dorsal margin broadly convex with somewhat steeper postero-dorsal slope; ventral margin nearly straight to slightly concave. Anterior is broadly rounded while the posterior is rather more truncate. Shell surface smooth. In dorsal view carapace somewhat compressed with maximum width medially; left valve slightly larger than right. Normal pore canals small and inconspicuous.

Internally cardinal angles more pronounced than externally. Shallow terminal vestibules are developed anteriorly and posteriorly. Muscle scar pattern consists of four unequal oval-shaped adductors.

Remarks. This species has been placed in the genus *Cypria* rather than *Cyclocypris* due to the compressed carapace in dorsal view and the larger left valve. The majority of species of *Cypria* are still living, and are largely distinguished on soft-part morphology. They show little affinity with the present species. Two fossil species which closely resemble *C. aqualica* are *C. tocorjescui* Hanganu (in Malz 1973*b*) and *C. dorsalta* Malz, 1973*b*, both Miocene forms from Germany. *C. tocorjescui* is distinctly subquadrate with a pronounced posterior cardinal angle and a convex ventral margin. *C. dorsalta* is quite distinct having a very highly arched dorsal margin.

Other fossil forms of *Cypria* include *C. anterosinuata* Staplin, 1963, a Pleistocene species from Illinois with a surface ornamentation of fine anastomosing lines; *C. nevadensis* Dickinson and Swain, 1967, a Plio-Pleistocene species from Nevada which is recognized on its truncated antero-dorsal slope; *C. parva* Grekoff, 1957, L. Cretaceous of the Belgian Congo, a small elongate species, and *C. subangulata* Chapman, 1896, a Pliocene form from California with, in dorsal view, distinctly compressed anterior margin. *C. pellucida* Sars, 1901 from Brazil is the Recent species closest to *C. aqualica*, but is distinguished from it by having a short truncated posterior margin and a projecting flange on the postero-ventral margin.

Family PARACYPRIDIDAE Sars, 1923
Genus PARACYPRIS Sars, 1866
Paracypris sp.

Plate 13, figs. 8–10

Material and distribution. Three adult single valves from the Pebas Beds of Pichua, Peru.

Dimensions. OS 11083 RV L 0·64, H 0·23; OS 11084 LV L 0·61, H 0·24; OS 11085 RV L 0·58, H 0·21.

Description. Non-dimorphic carapace elongate, subtriangular in lateral view with broadly arched dorsal outline tapering to a ventrally situated pointed posterior and rounded anterior margin; ventral margin slightly concave. Greatest height occurs just anterior to mid-point, greatest length ventral. Valves compressed; valve surfaces smooth. Duplicature very wide anteriorly, slightly less wide posteriorly with large irregular terminal vestibules. Marginal pore canals and muscle scars not seen. Hinge adont, dorsal margin of right valve fitting into a groove in the larger left valve.

Remarks. Insufficient material is available for formal specific identification. *P. labocana* Bold, 1972 from the Panama Canal differs in having a straight ventral margin and a more broadly rounded anterior margin. Although the characteristic bifurcating marginal pore canals have not been seen, this species is placed in *Paracypris* because it is otherwise similar in shape and size (*Macrocypris* is much larger). Preservation is poor. Since they were marine forms they were probably washed into the depositional area, rather than being indigenous.

Superfamily DARWINULACEA Brady and Norman, 1889
Family DARWINULIDAE Brady and Norman, 1889
Genus DARWINULA Brady and Robertson, 1885
Darwinula sp.

Plate 13, fig. 7

Material and distribution. One single valve and a few fragments only, from the Pebas Beds of Pichua, Peru.

Dimensions. OS 1055 RV L 0·51, H 0·21.

Description. Shell elongate, ovate, rounded anteriorly and posteriorly with straight, parallel dorsal and ventral margins. Maximum length occurs medially; maximum height just posterior to mid-point. Shell surface smooth and featureless. Muscle scars typical *Darwinula*-type rosette of scars, precise number of which it is impossible to see. Hinge simply adont.

Remarks. The presence of *Darwinula* sp. in the Pebas sample is indicative of a fresh to brackish-water environment. It is unlikely that extensive transport of the specimens has taken place because the fragile valves are complete. This species is left under open nomenclature because of the lack of material.

Family PONTOCYPRIDIDAE G. W. Müller, 1894

Genus PONTOCYPRIS Sars, 1866

Pontocypris? sp.

Plate 13, figs. 11–15

Material and distribution. A few valves, only in the Pebas Beds of Pichua, Peru.

Dimensions. OS 11023 RV L 0·70, H 0·34; OS 11024 LV L 0·59, H 0·29; OS 11025 RV L 0·55, H 0·28; OS 11026 LV L 0·59, H 0·29; OS 11027 RV L 0·56, H 0·28.

Description. Shell elongate subtriangular with maximum height just anterior of the mid-point, greatest length ventrally. Dorsal margin strongly arched with a steep antero-dorsal slope to broadly rounded anterior margin; postero-dorsal slope tapers to posterior cardinal angle and then slopes steeply to posterior valve margin. Ventral margin slightly concave. Entire valve margins smooth, as are valve surfaces. Sexual dimorphism unknown. Internally inner margin very narrow with slight vestibules anteriorly and posteriorly. Marginal pore canals not seen but were probably very short. Hinge apparently adont. Muscle scars not seen.

Remarks. Insufficient material of this species is available for a specific name to be assigned to it. The generic name is queried mainly because of the very narrow duplicature; true *Pontocypris* species have a very wide anterior duplicature and narrower posterior duplicature. The genus usually has spines on the postero-ventral margin of the right valve only, which are absent in the present species. *Propontocypris* differs by having the greatest valve height medially. Although no complete carapaces have been found of *Pontocypris*? sp. the left valve appears to be the larger valve (by the presence of a marginal groove, at the posterior and anterior ends, that serves to accommodate the free edge of the right valve). In *Pontocypris* and *Propontocypris* the larger valve is the right valve. We suggest that *Pontocypris*? sp. may in fact belong to a genus closely related to *Pontocypris*: more material will have to be obtained to confirm this.

EXPLANATION OF PLATE 13

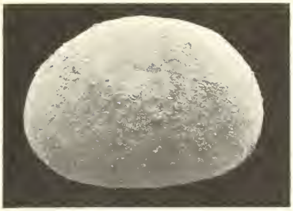
Figs. 1–6. *Cypria aqualica* sp. nov., Pebas Beds, Peru. 1, external view, left valve, holotype, OS 11016, ×75. 2, internal view, left valve, paratype, OS 11018, ×75. 3, dorsal view, carapace, paratype, OS 11019, ×77. 4, external view, right valve, paratype, OS 11017, ×75. 5, 6, external and internal views, juv. left valve, paratype, OS 11020, ×75.

Fig. 7. *Darwinula* sp., Pebas Beds, Peru, right valve, OS 11055, ×76.

Figs. 8–10. *Paracypris* sp., Pebas Beds, Peru. 8, external view, left valve, OS 11084, ×76. 9, external view, right valve, OS 11085, ×76. 10, internal view, right valve, OS 11083, ×76.

Figs. 11–15. *Pontocypris*? sp. Pebas Beds, Peru. 11, external view, right valve, OS 11023, ×76. 12, internal view, left valve, OS 11024, ×76. 13, external view, left valve, OS 11026, ×76. 14, 15, internal view, right valve, ×76, and hinge, ×150, OS 11025.

PLATE 13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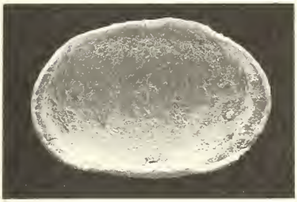
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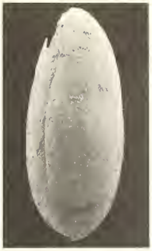
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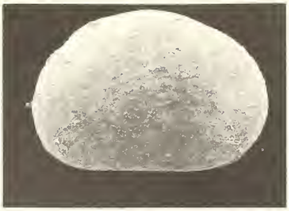
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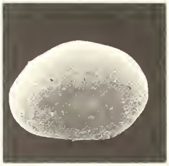
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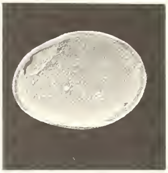
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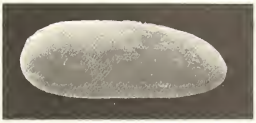
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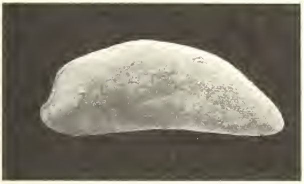
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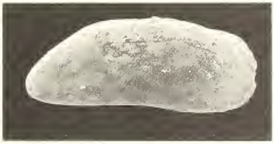
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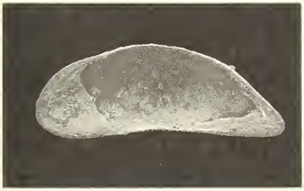
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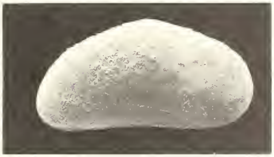
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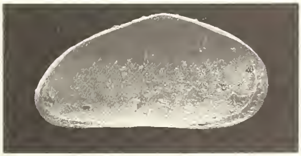
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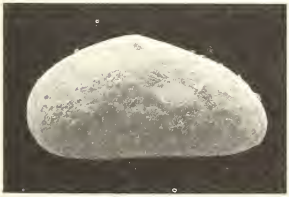
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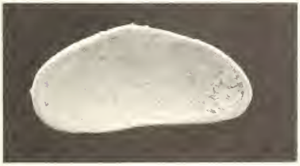
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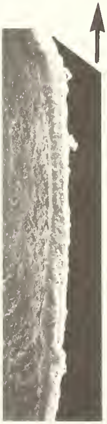
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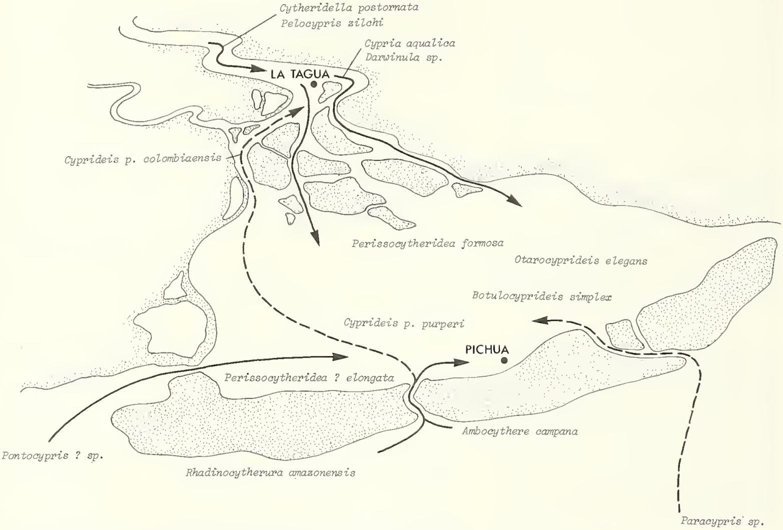
SHEPPARD and BATE, Plio-Pleistocene ostracods

ENVIRONMENT OF DEPOSITION

Of the three samples examined, the one from locality CAE/GEO/54, a grey clay full of crushed molluscs contained a fauna limited to a single ostracod species—*Cytheridella postornata* sp. nov. Although a large species, the shell is thin and delicate and no extensive transport of the material is envisaged. As *Cytheridella* is a freshwater genus there is no reason to regard the grey clay exposed on the river bank south of La Tagua as being anything other than a freshwater, possibly lake deposit. The other two samples, however, contain an ostracod fauna which is mixed both in variety of genera and species and in salinity tolerance. Although brackish, freshwater, and marine ostracods are all represented, the faunas of the Pebas Beds of Peru and from locality CAE/GEO/33 of Colombia are both dominated by the brackish-water species *Cyprideis purperi* sp. nov. of which two subspecies are recognized.



TEXT-FIG. 5. Palaeogeographic interpretation of the brackish-water lagoon environment in the Pebas and La Tagua regions during the Plio-Pleistocene.

Associated with *C. purperi purperi* subsp. nov. in the Pebas Beds are the new ostracods *Otarocyprideis elegans* gen. et sp. nov. and *Botulocyprideis simplex* gen. et sp. nov. both belonging to the same family as *Cyprideis* and considered to have inhabited a similar brackish-water environment. Like *C. purperi* they are represented by juvenile instars and are considered to have lived on the sediments in which they are now found. Two further brackish-water forms, both species of *Perissocytheridea*, *P. formosa* sp. nov. and *P.? elongata* sp. nov. are present in the Pebas Beds. *P. formosa* is the only brackish-water species that is found associated with *C. purperi colombiaensis* subsp. nov. in the Colombian sample CAE/GEO/33. Two shallow-water marine species present in both

Colombia (locality CAE/GEO/33) and Peru are *Ambocythere campana* sp. nov. and *Rhadinocytherura amazonensis* gen. et sp. nov. It is only at Pichua in the Pebas Beds that the deeper-water marine *Paracypris* is found, admittedly as a rare representative of the total fauna; the marine *Pontocypris* sp. is slightly more common in the Pebas Beds.

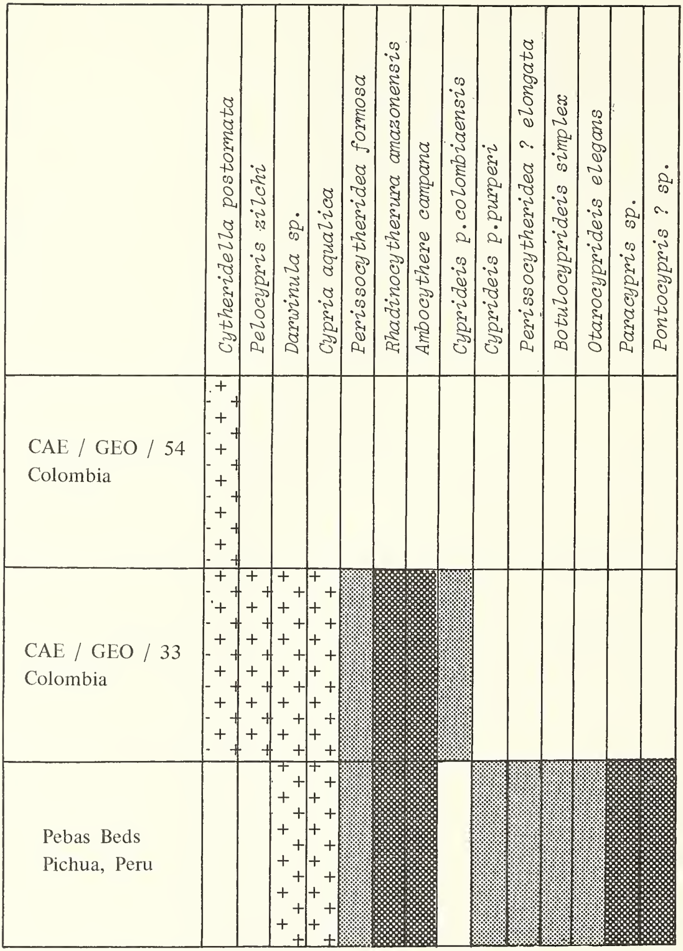
At the opposite end of the salinity gradient (see text-fig. 6) the Colombian locality CAE/GEO/33 has a larger freshwater ostracod fauna than does the Pichua sample of Peru with *Cytheridella postornata* sp. nov., *Pelocypris zilchi* Triebel, *Darwinula* sp., and *Cypria aqualica* sp. nov. Only *Darwinula* sp. and *C. aqualica* occur at Pichua. Thus we have two areas under consideration, the first in Colombia represented by locality CAE/GEO/54 with an entirely freshwater fauna and locality CAE/GEO/33 with a larger freshwater fauna associated with brackish and shallow marine ostracods. The second area is that of northern Peru in the region of Pichua where both the brackish-water and the marine elements of the fauna are increased. Text-fig. 5 illustrates our interpretation, though probably oversimplified, of the environment during the Plio-Pleistocene, with a marine transgression, possibly from the east, extending into the Pichua–La Tagua region, La Tagua being situated furthest from the sea. We consider, therefore, that the ostracods present in the Plio-Pleistocene deposits of La Tagua and Pichua reflect a series of different environments that belong, in our opinion, to a slow-moving river system having freshwater lakes on the flood plain and passing into the sea through a series of brackish-water lagoons. The lagoons would have been separated from the sea by islands and sand bars, the sea entering and the river flowing out through narrow channels.

Within the river system the slow movement of the water would permit the development of sand bars and the silting up of river channels would enable the brackish-water lagoons to develop. Freshwater lakes on the flood plain would support the *Cytheridella postornata* fauna while the other freshwater ostracods *Cypria aqualica*, *Pelocypris zilchi*, and *Darwinula* sp. would be equally at home in either still or very slow-moving water.

Saline conditions in a region of low relief exert an influence some distance from the sea to produce a brackish-water environment. Whether marine ostracods would be able to extend very far inland would depend on the strength of the freshwater flow in the opposite direction (although in tidal estuaries the incoming sea water does not mix but flows in over the outgoing fresh water), the strength and extent of the tidal flow, and the ability of the ostracods in question to survive in water of a lowered salinity. Significantly, those ostracods known to be solely marine in habit (in this case *Paracypris* sp.), occur only in the Pichua area, considered to have been fairly close to the sea—it is unlikely that purely marine ostracods such as *Paracypris* could survive for long in a brackish-water environment. Certainly *Paracypris* is a very rare member of the fauna. Such extensive transportation would also result in the sorting out of any larger marine species.

We have not been able to undertake a detailed palaeogeographical reconstruction of the area based on three samples but we do consider that the presence of brackish-water lagoons on the edge of a purely marine environment is the only rational interpretation of the geology. A sedimentological study of the region would be rewarding in terms of confirming the postulated direction of river flow from the north-west to the east and south-east. Thus, with land to the west and north-west the open sea would have lain to the east, the marine transgression entering along the present-day Amazon Basin. With the Andes to the west it is unlikely that any marine transgression could have entered from that direction. The surface topography during Plio-Pleistocene times could not have differed very much from what it is today where the whole of the Amazon Basin, from the headwaters in Peru and S. Colombia to the mouth of the river, lies within a height range of from sea-level to 200 metres. Little fluctuation in land and sea-level would be needed to bring marine conditions into the Peru/S. Colombia area.

In conclusion, we can state that the study of the ostracods has enabled us not only to suggest an age for the deposition of the sediments (see next section) but has revealed a much more complex situation than has generally been understood before. The presence of freshwater and of brackish-water ostracods is of less importance than is the occurrence of marine ostracods, for it is these that point to the presence, at that time, of a substantial marine transgression in the Plio-Pleistocene. The



TEXT-FIG. 6. Correlation and environmental chart of Colombian and Peruvian ostracods. Columns with dark stipple denote marine species; lighter stipple denotes brackish-water species and crosses denote freshwater species.

alternative explanation, that a series of brackish-water lakes existed and that the more marine ostracods were introduced at the egg stage by way of the feet or plumage of wading birds is not considered to be practicable. Certainly the presence of the deeper-water *Paracypris* would not support this hypothesis.

AGE AND CORRELATION

The basis for regarding the ostracod fauna as being of Plio-Pleistocene age rests primarily with the occurrence, in the Colombian material, of *Pelocypris zilchi*, a freshwater ostracod described from the Pleistocene of El Salvador. The complete geographical range of this ostracod is not known but its association, again in Colombia, with *Cytheridella postornata*, *Cytheridella* being a Pleistocene to Recent genus, again supports a Pleistocene age determination. The remainder of the fauna whether it be brackish, freshwater, or marine does not offer such precise information but certainly points to a late Tertiary age. Because we are dealing with faunas containing marine ostracods, and the necessity of envisaging a marine transgression to get them into the Upper Amazon, we consider that a late Pliocene to early Pleistocene age would be more accurate for these sediments.

The Colombian and the Peruvian samples are of the same age, based on the similarity of the ostracod faunas. Correlation of the two Colombian samples (text-fig. 6) is effected by the common occurrence of *C. postornata*, while correlation with the Pebas Beds of Pichua is possible through a larger fauna of fresh, brackish, and marine ostracods.

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THE TEMNOSPONDYL AMPHIBIAN *DENDRERPETON* FROM THE UPPER CARBONIFEROUS OF IRELAND

by ANDREW R. MILNER

ABSTRACT. The temnospondyl amphibians *Erpetocephalus rugosus* Huxley and *Ichthyerpeton hibernicum* Lydekker from the Jarrow Coal (Westphalian A) of the Leinster coalfield in Eire represent a single species referable to the genus *Dendrerpeton*, namely *D. rugosum* (Huxley) comb. nov. *D. rugosum* is very similar to the slightly later *D. acadianum* from Nova Scotia, the palate and pectoral girdle of which are reinterpreted. The genotype species of *Ichthyerpeton*, *I. bradleyae* Wright and Huxley, also from the Jarrow Coal, is considered to be based on an indeterminate, though probably temnospondyl specimen, and the binomen is hence a *nomen dubium*.

The genera *Dendrerpeton*, *Eugyrinus*, and *Caerorhachis* share only primitive or unassessable temnospondyl character-states with each other and with the 'long-snouted' edopoids. The Dendrerpetontidae is therefore removed from the Edopoidea, and *Eugyrinus* and *Caerorhachis* are excluded from the Dendrerpetontidae which is thus restricted to *Dendrerpeton*. On the evidence available, *Eugyrinus* is an early offshoot of the Trimerorhachoidea, while *Caerorhachis* and the Dendrerpetontidae are primitive temnospondyls of uncertain relationships.

UPPER Carboniferous amphibians and fishes were discovered at Jarrow Colliery in the Leinster coalfield in Eire in 1864 by W. B. Brownrigg (Brownrigg 1866). The amphibian assemblage collected at Jarrow is of historical significance in that it was the first assemblage of small coal-swamp amphibians to be described. The amphibian material from the previously discovered but similar assemblage from Linton, Ohio, was not interpreted as such until Huxley's (1867) description of the Jarrow animals made comparison possible. Many of the subsequently discovered small amphibians from the Upper Carboniferous of Newsham, Northumberland and Nýřany, Czechoslovakia were initially described with reference to the Jarrow material. However, since the initial descriptions of the Jarrow amphibians by Wright and Huxley (1866), Huxley (1867), Baily (1876, 1879, 1884), and Woodward (1897), very little first-hand study of this material has been undertaken. Most of the specimens have never been described because, although usually consisting of articulated skeletons, they are very poorly preserved. The substrate in which the animals were initially buried appears to have been of such a low pH as to mobilize most but not all of the skeletal calcium phosphate after burial (Rayner 1971, p. 452). Most specimens are little more than vague outlines on cleavage planes in the coal but some are preserved with visible detail indicating that the degree of bone solution varied from individual to individual.

The significance of the Jarrow fauna has increased with the identification of the Jarrow Coal as Westphalian A in age (Eagar 1961, 1964). The amphibian assemblage is thus distinctly older than the comparable assemblages from Mazon Creek, Illinois; Linton, Ohio, and Nýřany, Czechoslovakia, all of which are Westphalian D in age.

Most of the determinate amphibian specimens in the Jarrow assemblage are nectrideans and aïstopods, few temnospondyl specimens having been identified. A natural cast of a loxommatid skull was first described as *Anthracosaurus edgei* by Baily (1884) but has recently been shown by Beaumont (1977) to be referable to *Megalocephalus pachycephalus*. A small temnospondyl was described as *Erpetocephalus rugosus* by Huxley (1867) and, from another specimen, as *Ichthyerpeton*

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hibernicum by Lydekker (1891). It has been referred to the Dendrerpetontidae by Romer (1945, 1966) and is redescribed in this work as a species of *Dendrerpeton*. The genotype of *Ichthyerpeton* is *I. bradleyae* Wright and Huxley, 1866, also from Jarrow, and the identity of this specimen is discussed here. Other undescribed temnospondyls from Jarrow are currently being studied by the author and will be described in due course.

Specimen numbers preceded by the following abbreviations refer to material in the respectively listed collections: AMNH: American Museum of Natural History, New York; BM(NH): Department of Palaeontology, British Museum (Natural History), London; DMSW: D. M. S. Watson collection, Cambridge University Museum of Zoology; MCZ: Museum of Comparative Zoology, Harvard; MM: Manchester Museum; NMI: National Museum of Ireland, Dublin; RM: Redpath Museum, McGill University, Montreal; SM: Sedgwick Museum, Cambridge.

SYSTEMATIC DESCRIPTION

Class AMPHIBIA
Order TEMNOSPONDYLI
Family DENDRERPETONTIDAE Frič, 1885

Diagnosis. As for *Dendrerpeton*; see remarks under generic diagnosis.

Genus DENDRERPETON Owen, 1853

Type species. *Dendrerpeton acadianum* Owen, 1853.

Diagnosis. (Based on information in Carroll 1967 and authors' studies.) Primitive temnospondyls probably growing to about a metre in length. Dermal bones of skull with ornamentation of pitting, not striated. Lateral-line sulci absent from dermal roofing bones. Snout short. Otic notches large, deep, and ovoid. Septomaxillae present as separate ossifications within the external nares. Lachrymals extend from borders of external nares to orbit margins. Centres of ossification of jugals behind level of posterior edge of orbits but jugals extend forwards to suture narrowly with lachrymals. Intertemporals present. Maxilla extends back to contact quadratojugal. Postero-lateral tabular process and dorso-medial quadrate process border otic notch. Palatine rami of pterygoids extend anteriorly to approach or contact anterior end of cultriform process of parasphenoid. Interpterygoid vacuities rounded anteriorly and occupying about $\frac{3}{5}$ of skull width. Internal carotid foramina on parasphenoid. Vertebral centra poorly ossified, pleurocentra small paired elements. Interclavicle slightly antero-posteriorly elongate with fimbriated anterior edge. Humerus with entepicondylar foramen. Ilium with postero-dorsal extension.

Remarks on classification. The family Dendrerpetontidae was most recently diagnosed by Romer (1947) as a monotypic family based solely on *Dendrerpeton* Owen, 1853. Romer later (1966) expanded the family to include *Erpetocephalus* Huxley, 1867 and *Eugyrinus* Watson, 1921. *Caerorhachis* Holmes and Carroll, 1977 is doubtfully referred to this family by its authors. In the present study the Dendrerpetontidae is treated as a monotypic family comprising only *Dendrerpeton* (including *Erpetocephalus*). Neither *Eugyrinus* nor *Caerorhachis* appears to be immediately related to *Dendrerpeton* in that there are no derived characters uniquely shared with that genus. Both genera are hence excluded from the Dendrerpetontidae so as to preclude the implication of close relationship to *Dendrerpeton* (see Discussion, p. 135).

Dendrerpeton rugosum (Huxley) comb. nov.

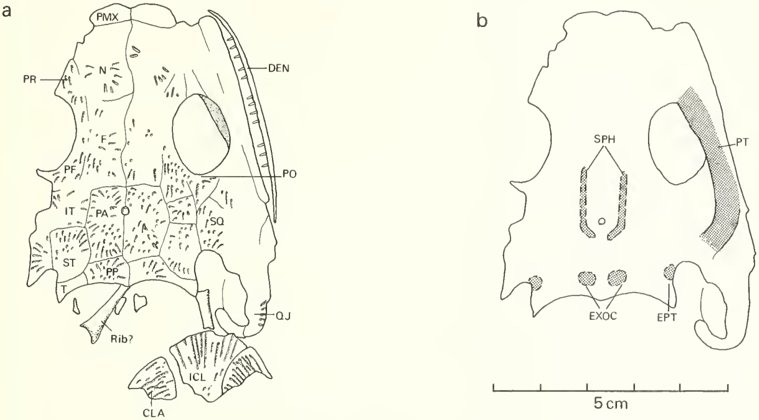
Text-figs. 1–3*a*, *b*

1867 *Erpetocephalus rugosus* Huxley, p. 368, pl. 23, fig. 2.
1890 *Ichthyerpetum bradleyae* Wright and Huxley; Lydekker, p. 169, *non* Wright and Huxley, 1866, Huxley, 1867—*Ichthyerpeton*.
1891 *Ichthyerpetum hibernicum* Lydekker, p. 343, figs. 1, 2.
1947 *Erpetocephalus rugosus* Huxley; Romer, p. 117.
1961 *Erpetocephalus rugosus* Huxley; Panchen and Walker, p. 326.

Diagnosis. As for genus, plus: jugal-lachrymal suture level with anterior margin of orbit. Snout very short, nasals as wide as, or wider than, own length. Tympanic notch large and nearly circular, almost as large as orbit.

Locality and horizon. All Jarrow Coal vertebrates were collected from the Jarrow Colliery about 7 km north-east of Castlecomer, Co. Kilkenny, Eire. The Jarrow Coal belongs to the lower *communis* zone, which is equated with the Westphalian A of the Upper Carboniferous (Eagar 1961, 1964).

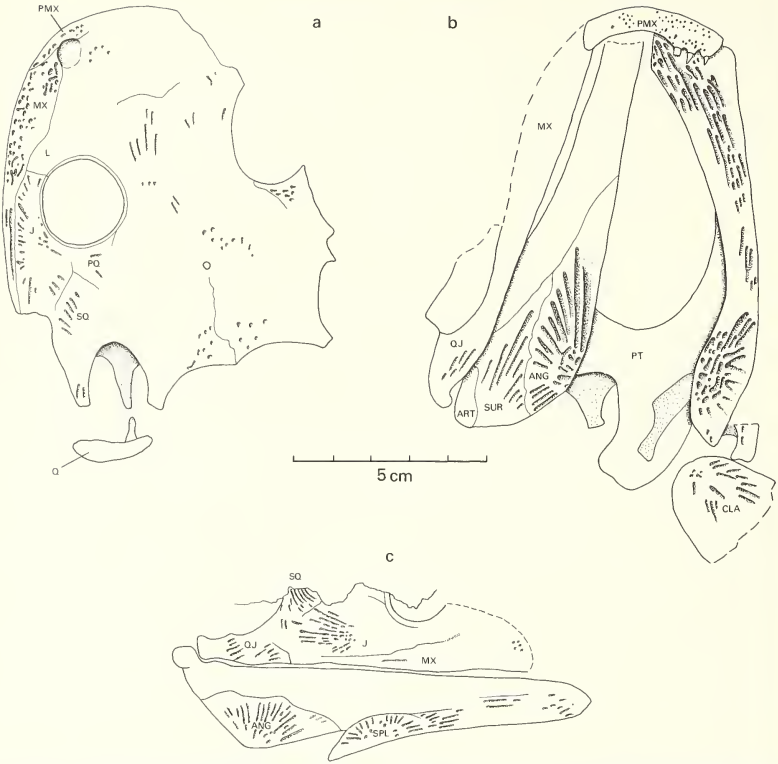
Holotype. NMI G39.1959, the holotype of *Erpetocephalus rugosus* consisting of a skull about 60 mm long, preserved in dorsal aspect with fragments of the pectoral girdle and ribs (text-fig. 1).



TEXT-FIG. 1. *Dendrerpeton rugosum* (Huxley) comb. nov., holotype, NMI G39.1959. *a*, specimen as preserved; *b*, diagram of skull roof showing pattern of ridges produced by underlying structures.

ABBREVIATIONS USED IN TEXT-FIGURES

ANG	Angular
ART	Articular
CLA	Clavicle
DEN	Dentary
ECT	Ectopterygoid
EPT	Ridge formed by Epipterygoid
EXOC	Ridge formed by Exoccipital
F	Frontal
ICL	Interclavicle
IT	Intertemporal
J	Jugal
L	Lachrymal
MX	Maxilla
N	Nasal
PA	Parietal
PAL	Palatine
PF	Postfrontal
PMX	Premaxilla
PO	Postorbital
PP	Postparietal
PR	Prefrontal
PSP	Parasphenoid
PT	Pterygoid
Q	Quadrate
QJ	Quadratojugal
SMX	Septomaxilla
SPH	Ridge formed by Sphenethmoid
SPL	Postsplenial
SQ	Squamosal
ST	Supratemporal
SUR	Surangular
T	Tabular
VOM	Vomer



TEXT-FIG. 2. *Dendrerpeton rugosum* (Huxley) comb. nov. *a*, dorsal aspect of NMI G3.1970, previously the holotype of '*Ichthyerpetum hibernicum*' Lydekker; *b*, ventral aspect of the same specimen; *c*, SM E19571, right cheek and mandible as preserved.

Referred material. NMI G3.1970, the holotype of *Ichthyerpetum hibernicum* consisting of a skull about 95 mm long exposed in both dorsal and ventro-lateral aspect as a result of preparation. A fragment of clavicle is present (text-fig. 2*a*, *b*). SM E19571, an undescribed specimen consisting of a skull mainly visible in palatal aspects but with the right cheek folded over and superimposed on the palate (text-fig. 2*c*).

Description

None of the specimens is well preserved although some surface detail can be seen on all of them. The proportions vary with size, and the description of the skull shape refers to the largest skull, presumed to be adult or most nearly so.

Skull. The skull is very short-snouted and the orbits are in the anterior half, their posterior margins being about half-way along the medial length of the skull. The orbits are circular but preservation is too poor to permit determination of the presence of a sclerotic ring. A pineal foramen is present in the anterior half of the suture between the parietals. The jaw suspensorium extends well behind the posterior edge of the skull table, and the otic notches are very large and deeply concave indicating the presence of large circular tympanic membranes. The tabular and quadrate extensions could have served to support the margin of a large tympanum. Typical temnospondyl-type pitting covers the dermal roofing bones, and no lateral-line pits or grooves are present.

Cranial dimensions (*in mm*)

	NMI G39.1959	SM E19571	NMI G3.1970
Skull tip to back of skull midline	61	–	95
Snout tip to quadrate	74	98	110
Tabular tip to tip width	30	–	43
Interorbital width	21	–	28
Orbit width	12·5	18	21
Extraorbital width	7	12	12

Dendrerpeton rugosum possesses all the dermal roofing bones typically found in primitive temnospondyls. The premaxilla is an antero-posteriorly narrow bone with no posterior extension against or near the medial edge of the external naris. The maxilla is deep anteriorly, but narrows sharply at the level of the anterior edge of the orbit and extends back as a narrowing ossification to suture with the quadratojugal at the level of the pineal foramen. The precise shape of the lachrymal is uncertain but it appears to extend from the external naris to the margin of the orbit. The jugal extends narrowly around the outer margin of the orbit to suture with the lachrymal just anterior to the level of the anterior margin of the orbit. Where it borders the orbit, the jugal is less than half the width of the orbit itself. The broad interorbital region is comprised of wide frontals and broadly suturing prefrontals and postfrontals. The postorbital is approximately equilaterally triangular in shape and not antero-posteriorly elongate. A rhomboidal intertemporal is present. The skull table is of typical temnospondyl configuration, the parietal and tabular being separated by a supratemporal-postparietal suture. The postparietals do not bear any superficial posterior extensions, often called postparietal lappets, such as occur in *D. acadianum* as small unornamented structures and in *Cochleosaurus bohemicus* as large ornamented structures. The tabulars extend outwards and backwards beyond the level of the postparietals, these extensions being square-ended in larger specimens (NMI G3.1970). The outer face of the squamosal is large and crescent-shaped bordering a deep, rounded otic notch. The quadratojugal extends from a narrow contact with the maxilla to the back of the jaw suspensorium. At its posterior end it apparently bears an extension behind the squamosal, although the poor preservation makes the relationships of the bones in this part of the skull difficult to ascertain. There is, however, a raised process which extends mesially or dorsomesially over the presumed position of the quadrate and forms a partial posterior border to the otic notch (text-fig. 2*a*). Comparison with similar structures in many temnospondyls of the superfamily Dissorophoidea suggests that this is a dorsomesial process of the quadrate (Bolt 1969). The tabular extension and the quadrate process both appear to be supports for the posterior margin of a large tympanum, and it is possible that the gap between the tabular and the quadrate process was bridged by an annular cartilage as in frogs.

The anterior part of the palate and parasphenoid are unknown. The interpterygoid vacuities are large, being comparable to those in the later Carboniferous and Permian temnospondyl family Dissorophidae, for example *Tersomius* and *Broiliellus* as figured by Carroll (1964, figs. 4, 10). The palatine ramus of the pterygoid is relatively narrow while the basipterygoid ramus is relatively broad.

The braincase is not visible, but indirect evidence of its general proportions is present in the holotype (text-fig. 1*b*). Post-burial flattening of the skull has compressed the skull table on to the underlying braincase and associated structures, producing a series of broken ridges where the dermal bones have been crushed upwards by underlying structures. Comparison with the skull of *Edops* (from Romer and Witter 1942) and *Amphibamus* (from Carroll 1964) suggests the following interpretation. The parallel ridges superimposed on the frontals and parietals and converging posterior to the pineal foramen appear to be the dorsal edges of the sphenethmoid, forming the sides of the braincase and converging, but not meeting, at about the level of the basipterygoid processes. The two raised structures posterior to these appear to have been produced by the paired exoccipitals. The two lateral raised structures appear from their position to have been produced by the ascending processes of the epipterygoids. None of the specimens shows preserved stapes, although the large tympanic notches indicate that these must have been present.

The lower jaw bears pronounced ornamentation on the angular, surangular, and splenials (text-fig. 2*c*) as in all primitive temnospondyls. The inner face is not visible on any specimen. The teeth are simple and conical but no quantitative assessment of the dentition is possible.

Pectoral girdle. The interclavicle has a complex anterior margin with a fimbriated anterior edge as in *D. acadianum*, *Eugyrinus wildi* (pers. obs.), and *Acroplous vorax* (Hotton 1959). This occurs frequently in small Palaeozoic amphibians. The interclavicle is substantially overlapped by the ovoid blades of the clavicles.

Remarks

D. rugosum is very similar to the type species of *Dendrerpeton* namely *D. acadianum* Owen from the Westphalian B tree-stump assemblages from Joggins, Nova Scotia. This material was reviewed by Carroll (1967), and the following comments are intended to supplement Carroll's description and to qualify the diagnoses given to distinguish the two species of *Dendrerpeton* in this study. The diagnostic characters are all that the material permits, *D. rugosum* consisting of three poorly preserved specimens while *D. acadianum* consists of many fragmentary and disarticulated specimens, not all of which are of certain attribution.

One distinguishing feature for the two species is the position of the lachrymal–jugal common suture. In *D. rugosum* this is level with the anterior edge of the orbit (text-fig. 2*a*, *c*), in *D. acadianum* it is level with the middle of the orbit and is little more than a point-contact (text-fig. 3*c*). The tendency to posterior withdrawal of the jugal and narrowing of its anterior process occurs in several other tetrapod groups and, as a trend, culminates in complete separation of the lachrymal and jugal, often with a dorsal process of the palatine occupying some of the intervening space (Bolt 1974). As noted by Bolt, this occurs independently in dissorophoids, saurerpetontids, and seymouriamorphs and is not, by itself, an indication of relationships between groups.

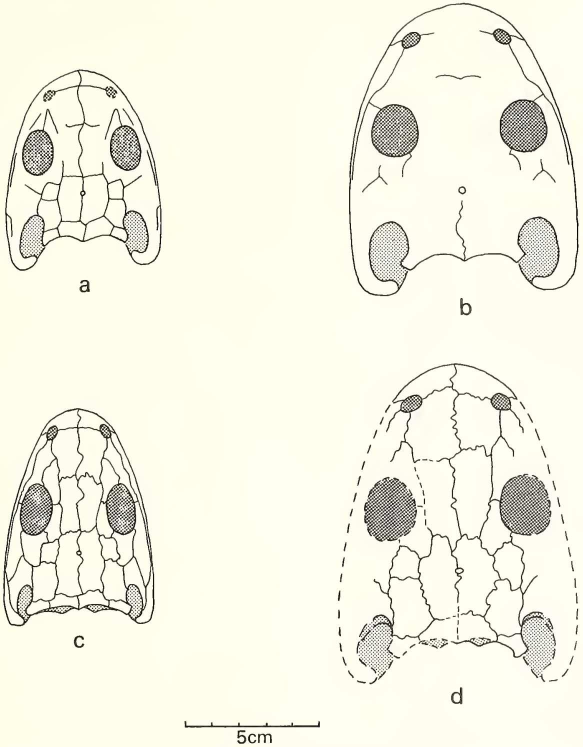
The other distinguishing features concern over-all proportions of the snout and the otic notch (text-fig. 3). Independent of absolute size, the snout of *D. rugosum* is shorter and the otic notches larger, than in *D. acadianum*. The skull of *D. rugosum* tends towards an *Amphibamus*-like shape.

Carroll's reconstruction of *D. acadianum* differs from *D. rugosum* in several other respects, but my examination of the *D. acadianum* material housed in the British Museum (Natural History), suggests that some of the characters of Carroll's *D. acadianum* reconstructions require qualification, as follows.

Postparietal lappets. These are not visible in *D. rugosum* specimens but can be seen in a minority of *D. acadianum* specimens and are depicted in the reconstruction by Carroll (1967, text-fig. 3B). As Carroll notes, the lappets are unsculptured and slope ventro-posteriorly from the lower posterior edge of the postparietal to support the exoccipitals. In this orientation the lappets can be seen only in specimens in which the occipital region is at least partly exposed (BM(NH) R.439 and R.4167). The non-visibility of such structures in the two Jarrow specimens with skull tables cannot be taken as proof of absence.

Postero-lateral development of the tabulars. These processes are pronounced in both species, and Steen (1934, text-fig. 11) depicts them on most skull tables, although Carroll (1967, text-fig. 3B) barely suggests their presence. Specimens such as BM(NH) R.436 (text-fig. 4*a*) show a very pronounced process and it is clear that both species of *Dendrerpeton* possess these processes. Another feature of the skull table of both species which Carroll does not depict in his reconstruction is the biconcave undulation of the back of the skull table. In all specimens where the skull table is well preserved, there is a shallow but distinct concavity in each half of the posterior edge above the postparietal lappets.

Palatal vacuities and pterygoid configuration. Carroll (1967, text-fig. 3C) depicts *D. acadianum* with interpterygoid vacuities which are antero-posteriorly elongate, almost parallel-sided, and bordered anteriorly by the undulating posterior edge of the vomers. However, BM(NH) R.4167 (text-fig. 4*b*) and DMSW B.45 (Watson 1956, fig. 30) show the palatine rami of the pterygoids to be markedly curved. Each interpterygoid vacuity must have been almost semicircular in outline and slightly broader and shorter than depicted by Carroll. In the palate of BM(NH) R.4167 (text-fig. 4*b*), an

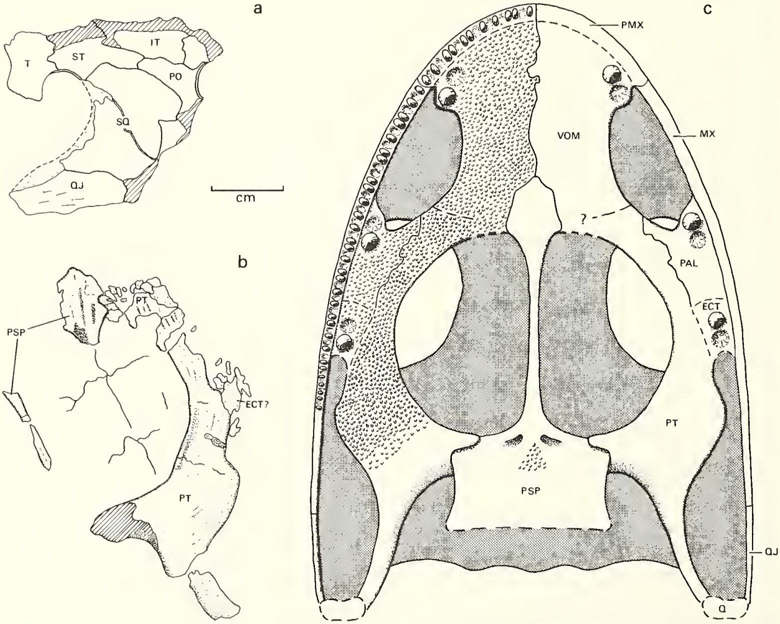


TEXT-FIG. 3. Reconstructions of *Dendrerpeton* skulls in dorsal aspect. *a*, *D. rugosum*, holotype specimen; *b*, *D. rugosum*, NMI G3.1970; *c*, *D. acadianum*, composite after Carroll 1967, text-fig. 3, with modifications; *d*, *D. acadianum*, BM(NH) R.4554. All to the same scale.

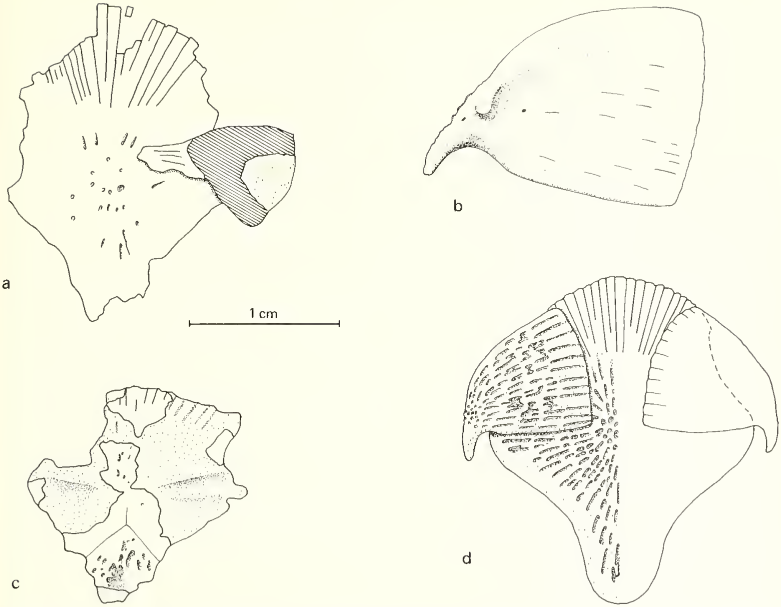
anterior median rhomboidal structure can be seen which I interpret, following Steen (1934), as an anterior expansion of the cultriform process of the parasphenoid. Although some crushing and displacement of the bones has occurred, striations on the lateral palatal series suggests that the pterygoid extends around the front of the interpterygoid vacuity and either approaches closely, or reaches, the cultriform process. A revised reconstruction of the palate of *D. acadianum*, modified from that of Carroll, is given in text-fig. 4*c*. The palatine is based on that in the lectotype skull BM(NH) R.4158 (Carroll 1967, text-fig. 2c). The general conclusion is that both species of *Dendrerpeton* possessed rounded interpterygoid vacuities only slightly smaller than those of primitive dissorophids such as *Amphibamus*, but with a more extensive anterior pterygoid border.

Pectoral girdle. The unconventional orientation of the clavicles on the interclavicle of *D. acadianum* reconstructed by Carroll (1967, text-fig. 13) is based on a misinterpretation of the pectoral girdle in BM(NH) R.436 (Carroll 1967, text-fig. 10; this paper, text-fig. 5*c*). In this specimen, the 'right clavicle' of Carroll is the fimbriated leading edge of the interclavicle and his 'left clavicle' is a symmetrical crack on the posterior process of the interclavicle, which is thus orientated at 90° to Carroll's interpretation and actually has no associated clavicles. The clavicles (text-fig. 5*a*, *b*) are broader-bladed than depicted by Carroll (1967, text-fig. 12c), and a suggested reconstruction of the interclavicle and clavicles is given in text-fig. 5*d*. This also corresponds with such of the pectoral girdle as is visible in the holotype of *D. rugosum* (text-fig. 1*a*).

In conclusion, first-hand study of the two assemblages of *Dendrerpeton* suggest that they are extremely similar and distinguishable only in the over-all shape of the skull and otic notch and the position of the lachrymal-jugal suture. Thus specific separation seems the most that can be justified, and the Jarrow material is maintained as a separate species. The two species of *Dendrerpeton* are not widely separated in time (mid Westphalian A for *D. rugosum* and early Westphalian B for



TEXT-FIG. 4. *Dendrerpeton acadianum* Owen, cranial anatomy. *a*, BM(NH) R.436, left temporal region in internal aspect, showing postero-lateral process of tabular; *b*, BM(NH) R.4167, incomplete parasphenoid and right pterygoid in dorsal aspect; *c*, reconstruction of skull in palatal aspect based on BM(NH) R.4158, R.4167, and RM2.1125.



TEXT-FIG. 5. *Dendrerpeton acadianum* Owen, clavicles and interclavicle. *a*, BM(NH) R.4553, interclavicle and fragmentary clavicle; *b*, reconstructed left clavicle in dorsal aspect based on both clavicles in BM(NH) R.4165 and R.4167 (counterparts); *c*, BM(NH) R.436, interclavicle, misinterpreted as interclavicle with overlapping clavicle blades by Carroll 1967, text-fig. 10; *d*, reconstruction of interclavicle and clavicles in ventral aspect, based on several specimens associated with *D. acadianum* skulls.

D. acadianum) and, during the early Westphalian, the localities in Ireland and Nova Scotia would have been about 1500 km apart in the pre-Atlantic Euramerica as depicted by Smith *et al.* (1973). It is thus a further example of a Carboniferous tetrapod genus showing a Euramerican distribution.

Expression of characters and growth in Dendrerpeton

Because of the small size of much of the *Dendrerpeton* material, it has been suggested that it could be juvenile material of a much larger amphibian (Romer 1947, p. 111). Carroll (1967, p. 119) reports several growth-linked changes in the genus, including elongation of the antorbital region, relative reduction in orbit size, and lowering of the skull table. With the identification of the Jarrow amphibians as *Dendrerpeton*, it is possible to make further observations on some of the growth-linked changes in the genus.

The holotype of *D. rugosum* and the lectotype of *D. acadianum* are both skulls of about 60–70 mm midline length, and Carroll's composite reconstruction of a *D. acadianum* skull depicts one of about this size. However, individual specimens of both species possess skulls of about 100 mm midline length, which presumably belonged to animals which were adult or more nearly so. The largest *D. acadianum* skull is BM(NH) R.4554, which has a midline length of 102 mm but lacks the cheeks (text-fig. 3*d*). The 95 mm long skull of NMI G3.1970 from Jarrow (reconstructed in text-fig. 3*b*) is comparable. A comparison of these larger skulls with the smaller type skulls (text-figs. 3*a*, *c*) reveals that in each species there is an over-all growth pattern, comprising reduction in relative orbit size and an increase in relative width of the skull but no increase in antorbital skull length. There is no tendency to elongation of the nasals, prefrontals, and lachrymals such as occurs in the ontogeny of long-snouted temnospondyls, but there is relative widening of the nasals, the posterior region of the postfrontals, and the midline region of the parietals, so that in the larger individuals the anterior skull is broader in outline. The large, deep otic notch remains relatively large with size increase and the tympanum apparently required increased skeletal support in large individuals. As a result of these extensions, the tabular processes thicken and become 'square'-ended and the back of the skull table becomes concave. The jaw suspensorium continues to support the ventral edge of an enlarged tympanum by means of a dorsal process of the quadrate. As noted by Romer (1947) this is a similar situation to that in the dissorophids; in both cases this is the consequence of the possession of a large circular tympanic membrane.

Although the size range of *Dendrerpeton* skulls depicted in text-fig. 3 is limited, it demonstrates that no allometric snout elongation or skull table elongation occurs with growth. Hence, if *Dendrerpeton* did grow to a much larger size, it would not have come to resemble the 'long-snouted' edopoids but would have possessed a rounded short-snouted skull, like that of the largest known specimens but with relatively smaller orbits. The possession of a large tympanum which appears to have remained relatively large with over-all size increase suggests that the genus probably did not attain a much greater size than that recorded, otherwise the tympanum would have become too large a structure to be useful. Those amphibian lineages (e.g. the dissorophids and trematopids) which possess a relatively large tympanum do not attain a skull length much greater than 150 mm. I suggest, therefore, that the largest known *Dendrerpeton* skulls represent, or approach, the adult shape and size for the genus.

This emphasis on the configuration of the skull of the presumed adult of *Dendrerpeton* is particularly relevant to consideration of the phylogenetic position and relationships of the genus. The larvae and subadults of many temnospondyls are relatively similar to one another, as evidenced by the confusion engendered by 'branchiosaurs' over the last century. Lacking many of the adult specializations and fully expressed characters produced by local allometric growth, the larvae can be difficult to distinguish from one another, and it is possible to 'derive' a wide range of adults from a given juvenile either ontogenetically or phylogenetically if a time lag is involved. Carroll's reconstruction of *Dendrerpeton* (1967, text-fig. 3), being based on subadult material, shows little evidence of local allometric growth or specialization of the otic notch region and is a plausible 'ancestral form' for many temnospondyls. The similarity of subadult temnospondyls is evidenced by the fact that Frič (1885) referred several juvenile *Cochleosaurus* specimens to *Dendrerpeton* as *D. pyriticum* and *D. ?deprivatum*. Even Steen's reconstruction of the skull of *Cochleosaurus* (1938, text-fig. 30) is similar to *Dendrerpeton*, being based on 70-mm-long skulls, although *Cochleosaurus* grew to three times that skull length and acquired a considerably more elongate snout than depicted in Steen's reconstruction. The nearly ovoid skull of the adult *Dendrerpeton* and the superficially crocodile-like skull of the adult *Cochleosaurus* are far more distinct than the widely figured reconstructions of subadults would suggest. The significance of this in the determination of relationships of *Dendrerpeton* with other temnospondyls is that the adult material, though imperfect, may be more suitable for determination of relationships than the more completely available and more usually figured subadult material.

THE STATUS OF '*ICHTHYERPETON BRADLEYAE*' WRIGHT AND HUXLEY

1866 *Ichthyerpeton* Etheridge, p. 4, *genus coelebs*.
1866 *Ichthyerpeton bradleyae* Wright and Huxley, p. 168.
1867 *Ichthyerpeton bradleyae* Wright and Huxley, p. 367, pl. 23, fig. 1.
1890 *Ichthyerpetum bradleyae* Wright and Huxley; Lydekker, p. 168 (*Ichthyerpeton* emend.).
1947 *Ichthyerpeton bradleyae* Wright and Huxley; Romer, p. 266.
1970 *Ichthyerpeton bradleyae* Wright and Huxley; Panchen, p. 63, as *nomen vanum*.

Holotype. NMI G42.1959.

Referred material. Huxley (1867) refers NMI G.43.1959 here. Lydekker (1890) refers BM(NH) R.8453–8455 and R.8458–8459 here (see Panchen 1970, p. 63 for details). Because of the indeterminate nature of the holotype, all assignations of material are undemonstrable.

Locality and horizon. Jarrow Colliery, Castlecomer, Co. Kilkenny, Eire; *communis* zone, Westphalian A, Upper Carboniferous.

Remarks. In 1890 Lydekker suggested that *Erpetocephalus rugosus* was a junior synonym of *Ichthyerpeton bradleyae*. No subsequent author has accepted this synonymy but it is, perhaps, appropriate at this point to discuss the identity of the holotype of *I. bradleyae*.

The holotype specimen, which I have examined, consists of a poorly preserved articulated trunk and tail with pelvic girdle and hind limb present but no skull or anterior appendicular skeleton. There is about 105 mm of trunk present bearing twenty-eight presacral vertebrae, and 120 mm of tail which is incomplete. The trunk bears distinct chevrons of ventral dermal scales. As noted by Panchen (1970) the structure of the vertebrae cannot be determined, but they do not appear to be embolomerous. The holotype bears a general resemblance to undescribed colosteid material from this locality, and the presence of a long presacral column (twenty-eight presacral vertebrae posterior to the pectoral girdle) supports this possibility. However, the specimen could possibly belong to one of the other temnospondyl taxa which occur in the same assemblage and which are not known from articulated postcranial material. Most of Lydekker's referred specimens are equally indeterminate except for BM(NH) R.8453, an undescribed *Gaudrya*-like form and BM(NH) R.8455, a colosteid. Thus, the combination of poor preservation and the absence of associated cranial material renders the holotype of *I. bradleyae* indeterminate, and the binomen is a *nomen dubium* restricted to the holotype specimen.

DISCUSSION

Relationships of Dendrerpeton

Dendrerpeton *and the Edopoidea*. The superfamily Edopoidea, as used by Langston (1953), Carroll (1967), and Holmes and Carroll (1977), comprises a group of Carboniferous and Lower Permian temnospondyls which Langston places in four families: the Edopidae, Cochleosauridae, Chenoprosopidae, and Dendrerpetontidae. The former three families are comprised of 'long-snouted' forms while *Dendrerpeton* is a 'short-snouted' form. Romer's (1966) doubtful inclusion of the Colosteidae in the Edopoidea has not been endorsed by subsequent workers, and Romer later (1969) described the relationships of colosteids as problematical.

Most of the characters used to define the Edopoidea and to assign *Dendrerpeton* to this superfamily are primitive temnospondyl or even primitive tetrapod characters. Among these may be noted the presence of intertemporals, a movable basipterygoid–basisphenoid articulation, small–medium size interpterygoid vacuities, and a single occipital condyle. The association of *Dendrerpeton* with the 'long-snouted' edopoids is based substantially on an over-all primitive similarity rather than on derived characters. Likewise, the superfamily Edopoidea defined on the above characters would be a primitive grade rather than a clade. The 'long-snouted' families do, in fact, share a further suite of derived characters which support the contention that they are more closely related to each other than any is to *Dendrerpeton*. These will be discussed in a separate publication but include an ornamented septomaxilla incorporated into the skull roof, a prefrontal–jugal suture excluding the lachrymal from the orbit margin, and the postero-distal region of the jugal separating the maxilla from the quadratojugal. *Dendrerpeton* shares none of these characters and, if it is an edopoid, is the most primitive offshoot of the superfamily. This is not a new observation; Romer (1947), Langston (1953), and Carroll (1967) all observe that *Dendrerpeton* is not only one of the earliest 'conventional' temnospondyls (i.e. excluding the colosteids and the loxommatids), but is also a plausible 'near-ancestor' both for the 'long-snouted' edopoids and for the dissorophoid–eryopoid complex.

The only possibly derived character-state attributed to *Dendrerpeton* and the 'long-snouted' edopoids which might indicate relationship is the absence of lateral-line sulci in the dermal bones of the skull (Carroll 1967; Holmes and Carroll 1977). However, although no specimen of *Dendrerpeton* possesses lateral-line sulci, these structures are present in at least some edopoids. Langston (1953, p. 365 and fig. 5) describes lateral-line sulci and foramina in pit-bottoms in *Chenoprosopus*. I have examined a cast of the acid-etched specimen (AMNH 6954 from Linton, Ohio) depicted as '*Leptophractus obsoletus*' by Romer (1930, fig. 23 *right*), and this shows a clear series of lateral-line pits. They do not form a continuous sulcus but are present as unusually deep ornament pits, each with a basal foramen, and are visible on the right postfrontal, postorbital, intertemporal, and supratemporal. Thus, at least some edopoids possessed a buried lateral-line system in the skull, which is presumably a retention of the primitive tetrapod condition as seen in ichthyostegids. The absence of a lateral-line system in *Dendrerpeton* may simply be attributed to terrestriality as in the dissorophids rather than being indicative of close relationship to the 'long-snouted' edopoids.

Suggestions of an immediate relationship between *Dendrerpeton* and later 'advanced' temnospondyls have been based on the interpretation of the palate of *D. acadianum* as possessing large interpterygoid vacuities, pterygoids which do not extend to meet anteriorly, and a parasphenoid cultriform process which sutures with the vomers (Romer 1947; Langston 1953). As Carroll (1967) observes and as I have indicated in text-fig. 4*c*, the anterior part of the palate is not sufficiently preserved to permit its structure to be reconstructed with confidence in the area immediately anterior to the palatal vacuities. However, the interpterygoid vacuities in small specimens of *Cochleosaurus* are relatively smaller than in similar size specimens of *Dendrerpeton*, so that the large size of the interpterygoid vacuities does appear to be a size-independent character indicative of relationship to later dissorophoid and eryopoid temnospondyls. Further characters shared with the Dissorophoidea *sensu* Bolt, 1969 but not the Eryopoidea *sensu* Milner, 1978 are the anterior reduction of the jugal, particularly in *D. acadianum*, the large tympanic notch, and the apparent presence of a dorsal process on the quadrate.

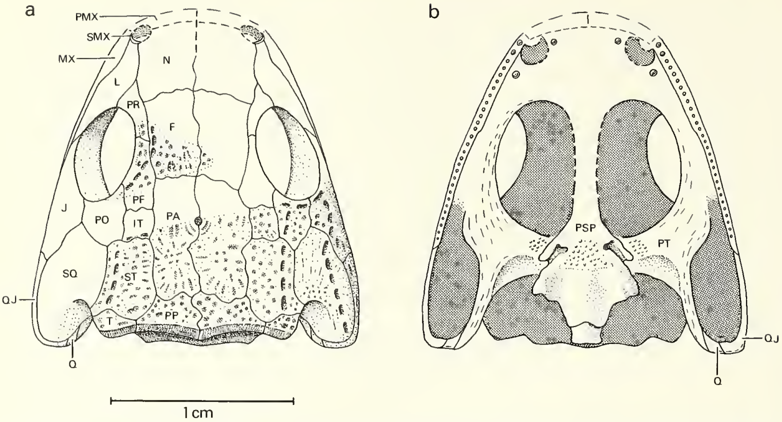
In conclusion, *Dendrerpeton* appears to share no derived character-states with the Edopoidea, and the presence of an undescribed *Gaudrya*-like edopoid in the Westphalian A of Jarrow indicates that *Dendrerpeton* is too late to be an ancestor to the 'long-snouted' Edopoidea. *Dendrerpeton* shares one derived character with the later 'advanced' temnospondyls such as the Dissorophoidea and Eryopoidea, and further characters with the Dissorophoidea alone. Neither the Dissorophoidea nor the Eryopoidea have been reported earlier than the Westphalian D. On the basis of this evidence I suggest that *Dendrerpeton*, with the family Dendrerpetontidae, be removed from the Edopoidea and be regarded as Temnospondyli *incertae sedis*, possibly as an early side-branch of the lineage leading to the dissorophoids.

Dendrerpeton, Caerorhachis, *and* Eugyrinus. Two other Carboniferous temnospondyls have an over-all similarity to *Dendrerpeton* and have been included in the Dendrerpetontidae. *Caerorhachis bairdi* Holmes and Carroll 1977 is doubtfully referred to the Dendrerpetontidae by its authors, and *Eugyrinus wildi* (Woodward) has been variously placed in the monotypic family Eugyrinidae by Watson (1940), in the synthetic family Peliontidae by Romer (1947), and in the Dendrerpetontidae, also by Romer (1966). Both monotypic genera are based on single, small, incomplete specimens and consequently both are imperfectly known and their relationships correspondingly difficult to assess. The following observations are based on Holmes and Carroll's description of *Caerorhachis* and on my own examination of *Eugyrinus*.

C. bairdi, probably from the Namurian A of Scotland, was first described by Holmes and Carroll (1977). It has an over-all primitive similarity to *Dendrerpeton* but differs from it in several fundamental respects. *Caerorhachis* appears to lack an otic notch, a prominent structure in *Dendrerpeton*, and the interpterygoid vacuities are much smaller, with the broad anterior rami of the pterygoids meeting extensively anteriorly. If the absence of the otic notch is the primitive condition as seen in colosteids (Panchen 1975, p. 611; 1977, p. 314), then *Caerorhachis* may be more primitive than any other non-colosteid temnospondyl. The broad anterior rami of the pterygoids and the small interpterygoid vacuities in such a small skull represents a more primitive palatal condition than occurs in *Dendrerpeton*, *Eugyrinus*, or the edopoids. Only in *Edops* is there a short anterior contact of pterygoids with broad anterior rami, and in that genus this condition can be attributed to the very large absolute size and the broad pre-orbital region of the snout. The vertebrae of *Caerorhachis* are unusual for a temnospondyl in that the pleurocentrum is large and 'horseshoe-shaped' and the overall construction is not rhachitomous but resembles that in the primitive batrachosaurs *Gephyrostegus* and *Proterogyrinus*. As Holmes and Carroll (1977) and Panchen (1977) observe, this vertebral construction could be interpreted as a primitive condition for temnospondyls or as a derived condition, functionally convergent with that of the primitive batrachosaurs. If the vertebral construction is primitive, it indicates that *Caerorhachis* is substantially more primitive than all the rhachitomous forms including *Dendrerpeton* and the 'long-snouted' edopoids. If the vertebral construction is a derived specialization within the Temnospondyli, it is unique within that group and gives no indication as to the relationships of *Caerorhachis*. The morphology of *Caerorhachis* admits of at least two interpretations of its phylogenetic position. One is that it is an extremely primitive small temnospondyl, the absence of an otic notch and the presence of gastrocentrous vertebrae indicating an offshoot of the temnospondyl line which is not only pre-*Dendrerpeton* and pre-edopoid but quite possibly pre-loxommatoid as well. If this interpretation is correct, it cannot reasonably be included in the Dendrerpetontidae or the Edopoidea unless these taxa are to be used as 'dustbin' taxa for generalized small early temnospondyls. An alternative interpretation is that *Caerorhachis* represents the juvenile of a large *Edops*-like form. The configuration of the pterygoids, the medio-dorsally angled articulating surface of the articular bone, and the suggestion of 'canine peaking' in *Caerorhachis* are consistent with this interpretation. Small skulls of *Cochleosaurus* from Nýřany possess relatively short snouts compared to the largest skulls (Steen 1938), so the short snout of *Caerorhachis* need not preclude such an interpretation. Because of the incomplete nature of the only skull, the apparent absence of an otic notch is not so obvious as to preclude this interpretation either. The vertebral construction remains a character of uncertain significance. On this interpretation, *Caerorhachis* could either be a juvenile 'long-snouted' edopoid such as *Edops* or a juvenile of a more primitive edopoid-like temnospondyl. It does not appear to share any derived characters with *Dendrerpeton* and there is no basis for placing it in the same family. It seems preferable to refer *Caerorhachis* to Order Temnospondyli *incertae sedis* at a primitive, possibly pre-loxommatid level, rather than to assign it to any of the presently established families or superfamilies of temnospondyls and to imply relationships which cannot be demonstrated.

Our knowledge of *Eugyrinus wildi* derives from the single specimen MM.W1222 from the Westphalian A of Colne, Lancashire, although there is also an undescribed '*Eugyrinus*-like' skull from the Westphalian A of Parrsboro, Nova Scotia (Carroll *et al.* 1972, p. 63). *E. wildi* has been successively described by Woodward (1891) and Watson (1921, 1940) and, being primitive and either juvenile or neotenous, it has been assigned to several higher taxa as an ancestral or near-ancestral form. Watson (1940) identified it as an early representative of a 'phyllospondyl'-anuran group, Romer variously referred to it as an early juvenile edopoid (1947, p. 116), an early juvenile trimerorhachoid (1947, p. 312), and later as a dendrerpetontid (1966). Chase referred to it as an early edopoid and not a trimerorhachoid (1965, p. 215), but later noted that it is an edopoid which is an ideal trimerorhachoid ancestor in most respects (1965, p. 220). Evidently both Romer and Chase considered the Edopoidea to be a primitive grade from which the Trimerorhachoidea emerged, with *Eugyrinus* somewhere in the continuum between the two.

Re-examination of the specimen permits a few new observations to be made. Contrary to



TEXT-FIG. 6. *Eugyrinus wildi* (Woodward), holotype and only specimen MM W1222. *a*, reconstruction of skull roof, composite of outer (ornament depicted) and inner surfaces as preserved; *b*, reconstruction of palate.

previous descriptions, the jugal extends forwards narrowly to contact the lachrymal outside the orbit (text-fig. 6*a*). Thus the maxilla does not border the orbit margin and *Eugyrinus* does not share that condition with *Branchiosaurus* as described by Watson (1940). Also unmentioned in earlier accounts is the presence of an incomplete sclerotic ring in the left orbit and an interclavicle with a fimbriated leading edge, as in *Dendrerpeton*.

Most of the characteristics of *Eugyrinus* are primitive or juvenile character-states which do not assist in determination of its relationships to other Palaeozoic temnospondyls. The short snout, the mobile basipterygoid–basisphenoid articulation, the intertemporals, and the single occipital condyle are all primitive temnospondyl character-states. Other features relate to its juvenile or neotenous condition. The narrow lachrymal-jugal contact, the absence of most palatal denticles, the simple dorsal blade of the ilium, the unossified vertebral centre, and the fimbriated leading edge of the interclavicle, are all characters associated with juvenile or small aquatic temnospondyls. Small specimens of *Dendrerpeton* possess a simple dorsal blade to the ilium (Carroll 1967, text-fig. 16c), while most small larval temnospondyls have proportionately narrower lachrymal–jugal contacts than the adults and also possess unossified vertebral centra (Boy 1972). The fimbriated anterior edge to the interclavicle occurs in diverse small amphibians such as *Branchierpeton*, *Acroplous*, and *Microbrachis*.

Eugyrinus shares with *Dendrerpeton* and most later temnospondyls the presence of large rounded interpterygoid vacuities but it appears to share no derived characters uniquely with *Dendrerpeton*. Unlike *Dendrerpeton*, *Eugyrinus* possesses prominent superficial lateral-line sulci on the skull, shallow but distinct otic notches, a parasphenoid with a slightly elongate basal plate narrowing anteriorly and posteriorly and bearing a medial ridge (all depicted in text-fig. 6), and a coronoid process on the lower jaw (Watson 1940, fig. 15). These are all derived characters reported in some or all of the Upper Carboniferous and Lower Permian trimerorhachoids (Chase 1965; Coldiron 1978) and suggest that *Eugyrinus* is most immediately related to the superfamily Trimerorhachoidea as suggested by Chase (1965, p. 220) and Carroll (1967, p. 132). Coldiron (1978) reports two further derived characters which *Eugyrinus* shares with the trimerorhachoid–brachyopoid complex, namely a broad cultriform process of the parasphenoid (which is not found in *Dendrerpeton*) and a retroarticular process of moderate length (which occurs in few early temnospondyls other than *Eugyrinus*, *Cacops*, and the trimerorhachoids). Because *Eugyrinus* lacks the anterior region of both the snout and the mandibles, it is not possible to ascertain whether or not it possessed the trimerorhachoid character of anterior palatal fenestrae and symphysial tusks. The Trimerorhachoidea as defined by Chase share further derived characters not possessed by *Eugyrinus* such as the relatively short limbs (those of *Eugyrinus* are fragmentary but not very reduced) and the secondarily elongate skull table (even in tiny *Saurerpeton* from Linton, Ohio). The elongation of the posterior region of the skull and the reduction of the tympanic notch in the families Trimerorhachidae, Saurerpetontidae, and Dvinosauridae, are here interpreted as secondary developments within a temnospondyl clade characterized by the possession of akinetic skulls and tympanic notches, rather than as direct retentions from primitively notchless labyrinthodonts with long, partly kinetic skull tables such as the Colosteidae. Some trimerorhachids, such as the *Trimerorhachis* specimens figured by Case (1935, fig. 3 and pls. 2–7) and Watson (1956), have shallow tympanic notches and slender dorso-laterally orientated stapes. The typical temnospondyl otic notch and stapes appear to be part of an impedance matching system for airborne sound reception and could be expected in terrestrial and amphibious forms, but not in aquatic specialists. It seems more economical to assume that the akinetic temnospondyl skull with deep otic notch and slender dorso-laterally orientated stapes evolved once and that the trimerorhachoids are secondary aquatics with a degenerate tympanic system and secondarily elongate skull, rather than to assume that the aquatic trimerorhachoids have inherited their elongate skull tables from primitive colosteid-like aquatic labyrinthodonts and have acquired otic notches and akinetic skulls independently of other temnospondyls.

On the basis of the characters of skull table length and reduced limbs, the trimerorhachoids are more closely related to each other than any is to *Eugyrinus*, but the characters which *Eugyrinus* does share with later trimerorhachoids indicates that it is an early offshoot of the trimerorhachoid–brachyopoid line. One unique feature possessed by *Eugyrinus* is, as noted by previous authors, the quadratojugal incorporated into the jaw articulation. The quadratojugal extends mesially behind and under the squamosal and partly replaces the quadrate on the articulatory surface (text-fig. 6*b*). There is no dorsal extension of the quadrate associated with tympanum support as there appears to be in *D. rugosum*. The unusual nature of the quadratojugal precludes *Eugyrinus* from ancestry to any known trimerorhachoid.

In conclusion, such derived characters as *Eugyrinus* possesses do not support an immediate relationship to *Dendrerpeton* despite an over-all primitive similarity, but indicate that *Eugyrinus* is an early offshoot within the Trimerorhachoidea *sensu* Chase, 1965. It is suggested therefore that *Eugyrinus* in the monotypic family Eugyrinidae be transferred to the superfamily Trimerorhachoidea.

SYSTEMATIC CONCLUSIONS

Dendrerpeton, *Caerorhachis*, and *Eugyrinus* are the earliest relatively unspecialized temnospondyls, only the extremely specialized colosteids and loxommatids having characters indicative of a more primitive origin. These three genera represent the primitive grade of small unspecialized temnospondyls and have been previously classified together, with some doubt, in the family Dendrerpetontidae on the basis of shared primitive characters. Their association with the 'long-snouted' edopoids in the superfamily Edopoidea has been on the same basis. The three genera do not, however, appear to share any derived characters with one another or with the 'long-snouted' edopoids and hence there is no evidence for immediate relationship among them. All three genera are removed from the Edopoidea, which is restricted to the contents of the families Edopidae and Cochleosauridae. Only *Eugyrinus* and the monotypic family Eugyrinidae can be assigned to another superfamily, namely the Trimerorhachoidea. *Caerorhachis* and *Dendrerpeton* are of indeterminate affinities, both probably being individual side-branches off the temnospondyl stem-lineage with *Caerorhachis* being distinctly more primitive than *Dendrerpeton*. The resultant classification is less tidy but represents the uncertainty of the relationships of these forms.

Order: TEMNOSPONDYLI

Superfamily: *incertae sedis, Caerorhachis bairdi*
Superfamily: Edopoidea, Families Edopidae, Cochleosauridae
Superfamily: Trimerorhachoidea, Family: Eugyrinidae
Eugyrinus wildi
Superfamily: *incertae sedis,* Family: Dendrerpetontidae
Dendrerpeton acadianum
Dendrerpeton rugosum

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THE EDOPOID AMPHIBIAN *COCHLEOSAURUS* FROM THE MIDDLE PENNSYLVANIAN OF NOVA SCOTIA

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ABSTRACT. A new species of the edopoid genus *Cochleosaurus*, *C. florensis*, has been found in the Westphalian D deposits of Nova Scotia. It differs from the Czechoslovakian species *C. bohemicus* in the sculpture pattern of dermal bones and in skull proportions. Morphologically, the skull of *Cochleosaurus* is intermediate between those of the edopoid genera *Dendrerpeton* (Westphalian B of Nova Scotia) and *Chenoprosopus* (Lower Permian of New Mexico).

IN 1956, a field party from the Museum of Comparative Zoology, Harvard, under the direction of the late Dr. A. S. Romer, excavated four of five fossil tree stumps at a new locality near Florence, Nova Scotia. Vertebrate fossils were found embedded in upright *Sigillaria* stumps that have been exposed by strip mining. The tree stumps are rooted above the Lloyd Cive seam of the Morian group, corresponding in age to the Westphalian D of Europe (Carroll *et al.* 1972). Stump number three produced most of the primitive captorhinomorph *Palaeothyris acadiana* (Carroll 1969), the limnoscelid amphibian *Limnostygis relictus* (Carroll 1967*b*) and several genera of primitive pelycosaurs (Reisz 1972), as well as two skulls of *Cochleosaurus*.

SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA
Subclass LABYRINTHODONTIA Owen, 1860
Order TEMNOSPONDYLI Zittel, 1887
Suborder RHACHITOMI Cope, 1882
Superfamily EDOPOIDEA Romer, 1945
Family COCHLEOSAURIDAE Broili, 1923
Genus COCHLEOSAURUS Fritsch, 1885
Cochleosaurus florensis n. sp.

Etymology. From the locality near Florence, Nova Scotia.

Holotype. MCZ 4343. Almost complete skull.

Referred specimen. MCZ 4344. Partial skull with well-preserved palate.

Horizon and locality. Morien group, equivalent to Westphalian C and D of Europe. Dominian Coal Co., strip mine No. 7, 2 miles north of Florence, Cape Breton County, Nova Scotia.

Diagnosis. An edopoid labyrinthodont assignable to the genus *Cochleosaurus* based on the presence of postparietal lappets, but distinct from the Czechoslovakian species *C. bohemicus* Fritsch, 1885, by smaller over-all size and by shorter postparietal lappets. The orbits are smaller, the snout is shorter, and the skull table is wider in *C. florensis* than in *C. bohemicus*.

Known distribution. Middle Pennsylvanian of eastern North America.

The edopoids are considered to represent a primitive stage in the evolution of rhachitomous amphibians (Romer 1947, 1966). They are characterized by the retention of the intertemporal, a movable palatobasal articulation, a single occipital condyle, and the absence of lateral line canals. The genus

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Cochleosaurus Fritsch, 1885, is characterized by the development of distinct posterior lappets on the postparietals. The pineal opening is present in juvenile specimens but is closed during subsequent growth (Steen 1938).

Both specimens of *C. florensis* (text-figs. 1 and 4) show a narrow, anteriorly rounded snout. The cheeks show a slight swelling, so that the lateral outline of the skull is fairly sigmoidal. The same is observed in the latex cast of the specimen of *C. bohemicus* (HMB 1902.1386b) available for study (text-fig. 4), but it is not shown in Steen's (1938) reconstruction of the skull of the latter species. Measurements taken from *C. florensis* (MCZ 4343) and *C. bohemicus* (HMB 1902.1386b) (Table 1) indicate the orbits of *C. florensis* to be somewhat smaller, the snout to be somewhat shorter in relation to the skull table but the skull table to be somewhat wider posteriorly.

In *C. florensis* the sculpturing of the dermal roofing bones of the skull consists of deep, rounded pits separated by high, narrow ridges the thickness of which is less than the diameter of the pits (text-fig. 1). Several depressed areas with subdued sculpturing are observed on the skull roof. Along the midline of the skull runs a band with less distinct sculpturing. The pits of this area are shallow, small, and rounded in outline and widely separated from each other. Elevated areas with strongly expressed sculpturing cover the temporal series of bones, surround the orbits, and continue anteriorly on the lateral halves of the nasals up to the posterior margins of the external nares. On the skull table, a level of intermediate height between the temporal bones and the mesial depression covers the lateral parts of the parietals and postparietals with an intermediate intensity of sculpturing. In the preorbital region, a depression with subdued sculpturing covers much of the lacrimal on either side. A high ridge running on the lateral parts of the nasal separates the lacrimal depression from the midline depression.

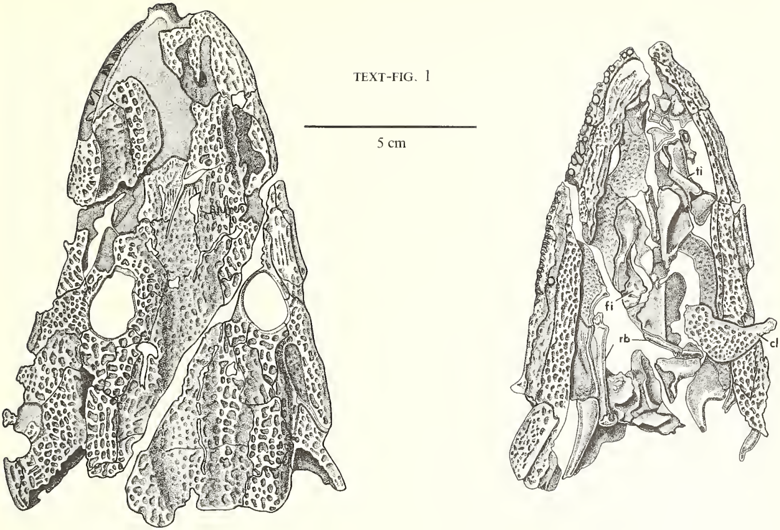
TABLE 1. Measurements taken on the specimens of *Cochleosaurus florensis* (MCZ 4343) and *C. bohemicus* (HMB 1902.1386b). All measurements in mm. Length of skull: from posterior margin of postparietal lappets to tip of snout; length of snout: from anterior border of orbit to tip of snout; length of skull table: from posterior margin of postparietal lappets to posterior margin of orbits; width of skull table: lateral edges of tabulars at posterior border; diameter of orbit: measured longitudinally.

	C. florensis	*C. bohemicus*
Length of skull	124	111
Length of snout	61	52·5
Length of skull table	44	39·5
Diameter of orbit	16	18
Width between orbits	25	17
Width of skull table	45	37
Index skull length: diameter of orbit	7·75	6·17
Index snout length: length of skull table	1·16	1·33
Index skull length: width of skull table	2·75	3
Index skull length: width between orbits	4·96	6·53

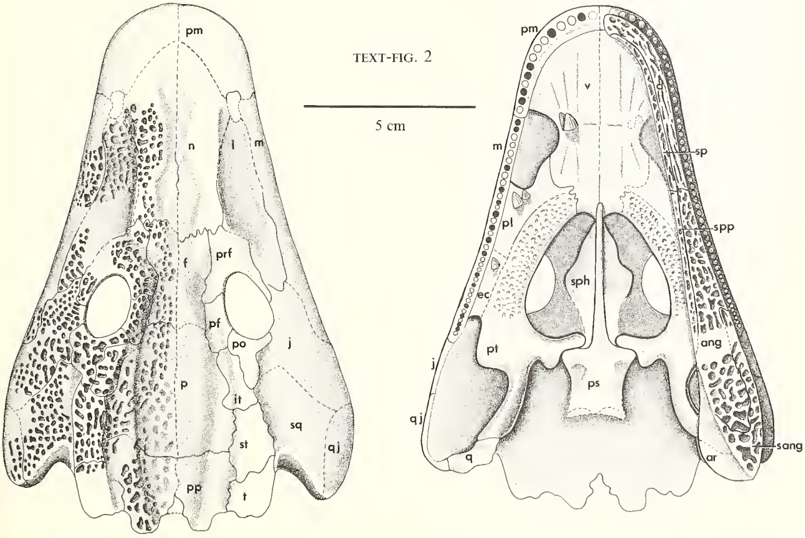
TEXT-FIG. 1. The skull of *Cochleosaurus florensis* (Holotype, MCZ 4343) in dorsal (*left*) and in ventral (*right*) view. $\times\frac{3}{4}$. Abbreviations: ang, angular; ar, articular; cl, cleithrum; ec, ectopterygoid; f, frontal; fi, fibula; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pl, palatine; plf, palatine fang; pm, premaxilla; po, postorbital; pp, postparietal; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; rb, ribs; sang, surangular; sp, splenial; sph, sphenethmoid; spp, postsplenial; sq, squamosal; st, supratemporal; t, tabular; ti, tibia; v, vomer; HMB, Museum für Naturkunde der Humboldt-Universität zu Berlin (DDR); MCZ, Museum of Comparative Zoology, Harvard University.

TEXT-FIG. 2. The reconstruction of the skull of *Cochleosaurus florensis* in dorsal (*left*) and in ventral (*right*) view. The interorbital space is interpreted as being vaulted, which accounts for a 10% loss in interorbital width as compared to text-fig. 1. $\times\frac{3}{4}$. Abbreviations as in text-fig. 1.

TEXT-FIG. 1



TEXT-FIG. 2



In *C. bohemicus* (HMB 1902.1386b) (text-fig. 4) the sculpturing of the dermal bones is also most pronounced on the temporal series of bones, around the orbits, and across the ossification centre of the nasals. There is subdued sculpturing along the midline of the skull roof, on the lateral margin of the parietal, and on the lacrimal. The ossification centre of the parietal is coarsely sculptured.

Thus a comparable pattern of intensified and subdued sculpturing exists in the two species of *Cochleosaurus*, but the specimen of *C. bohemicus* at hand lacks the depressions of the areas with subdued sculpturing. On the other hand, Fritsch (1885, table 60) figures another specimen of *C. bohemicus* with ridges running along the temporal series of bones and dorsal to the orbits, as well as on the lateral parts of the parietals and postparietals. The midline of the skull shows a somewhat weaker ridge. No difference between coarse and subdued sculpturing can be made out on Fritsch's (1885) plate, however. Somewhat similar ridges as those figured by Fritsch (1885) for *Cochleosaurus* are found in the genus *Zatrachys* (Langston 1953), although in a different arrangement.

One major difference between the two species of *Cochleosaurus* is that *C. florensis* shows uniformly shaped and distributed pits throughout, whereas *C. bohemicus* shows an elongation of the pits towards the margins of the dermal bones, most prominent in a longitudinal direction in the preorbital region and in a radial pattern on the cheeks. The elongate pits correspond to zones of intensive growth (Bystrow 1935) and indicate that the snout grows strongly in a longitudinal direction while the cheeks increase in width. The elongate pits are distinct in juvenile specimens but become obscured by subdivision when the animal is fully grown (Bystrow 1935). Thus it may be assumed that *C. florensis* was mature with a skull length of 124 mm (MCZ 4343), whereas the skull of *C. bohemicus* (HMB 1902.1386b) represents a still-growing juvenile at the length of 111 mm. *C. bohemicus* grows to 210 mm skull length at which size it has lost the juvenile pattern of ornamentation (Milner, pers. comm.). It appears that *C. bohemicus* would have reached a larger over-all size. This is considered as a species difference.

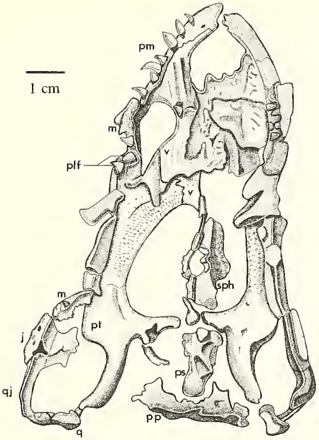
The postparietal lappets of *C. bohemicus* (HMB 1902.1386b) are more prominent than in *C. florensis* (MCZ 4343). Steen (1938) was able to show that the postparietal lappets show positive allometric growth during ontogeny. It thus appears that the adult *C. bohemicus* is characterized by much more prominent postparietal lappets than the smaller adult *C. florensis*.

The sculpturing of the lower jaw of *C. florensis* is characterized by large, irregular pits separated by high, narrow ridges on the angular and surangular. On the splenials, the pits tend to be smaller and shallower. On the dentaries, the sculpturing changes to a pattern of longitudinal ridges very different from the pitting on the other dermal bones. No lower jaw of *C. bohemicus* is available or well-enough figured to be used for comparison. In *Dendrerpeton* (Carroll 1967*a*), a condition similar to that of *C. florensis* is observed. Deep but elongate pits radiate to the margins of the angular bone. Pits on the splenial tend to be smaller. On the dentary, only shallow ridges are observed. In *Caerorhachis* (Holmes and Carroll 1977), evenly coarse sculpturing covers the lateral side of the lower jaw. The same appears to be true for *Chenoprosopus* (Langston 1953).

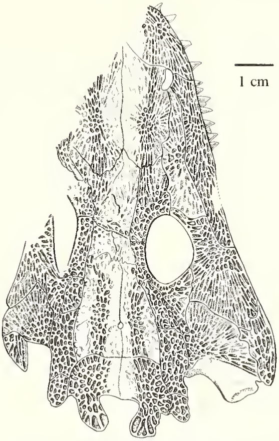
Because of the uniformity of the sculpturing, suture-lines separating the dermal elements of the skull are often difficult to follow in *Cochleosaurus florensis*. The pattern appears to be closely comparable to that in *C. bohemicus* (text-figs. 1 and 4). The lacrimal is excluded from the orbit by a narrow ventral process of the prefrontal which contacts the jugal. The jugal enters the lower margin of the cheek in *Cochleosaurus* but not in *Dendrerpeton* (Carroll 1967*a*). The postorbital typically consists of a broad anterior part bordering the orbit and a narrow, elongated posterior part lying between the intertemporal and the jugal which may reach the supratemporal bone posteriorly. The same arrangements are found in *Caerorhachis* (Holmes and Carroll 1977) and in *Dendrerpeton* (Carroll 1967*a*). Of the temporal series of bones, the supratemporal is the largest.

The palate of *Cochleosaurus bohemicus* is very poorly known (Broili 1905). It is well preserved in *C. florensis* (MCZ 4344), however, which serves as the basis for the following description (text-fig. 3).

The interpterygoid vacuities are wide, about one-sixth of the snout-quadrate length, but become narrower anteriorly. The palatine rami of the pterygoids converge anteriorly, but they do not meet in the midline anterior to the interpterygoid vacuities. They are bordered anteriorly by the vomers which



TEXT-FIG. 3. The palate of *Cochleosaurus florensis* (MCZ 4344) in ventral view. Natural size. Abbreviations as in text-fig. 1.



TEXT-FIG. 4. The skull of *Cochleosaurus bohemicus* (HMB 1902.1386b) in dorsal view. ×$\frac{3}{4}$.

form an interdigitating suture with the tips of the pterygoids and which enclose between them the tip of the cultriform process of the parasphenoid. In *Caerorhachis* (Holmes and Carroll 1977), a primitive edopoid with a shorter snout, the pterygoids meet anterior to the relatively narrow interpterygoid vacuities. This is probably the primitive condition. *Dendrerpeton* is generally considered to be somewhat more primitive than *Cochleosaurus* (Carroll 1967*a*). As restored by Carroll (1967*a*), the pterygoids in *Dendrerpeton* are less convergent anteriorly, which results in wider interpterygoid vacuities. However, in the text, Carroll (1967*a*) mentions the impossibility of determining the exact shape of the pterygoids. In *Chenoprosopus* (Langston 1953), the pterygoids form an interdigitating suture with the broadened tip of the cultriform process. This could be a secondary condition to reinforce the snout by bringing the anterior parts of the pterygoids near to the midline. *Cochleosaurus* is intermediate between *Dendrerpeton* and *Chenoprosopus* with respect to this character.

The quadrate ramus of the pterygoid is a high, blade-like structure with a narrow ventral edge. The jaw articulation lies between the occipital condyle and the occipital plane of the skull roof. The quadrate ramus of the pterygoid, the quadrate, the quadratojugal, the jugal, and the posterior part of the maxilla bordering the subtemporal fossa, all have their ventral edges on the same plane.

Of the braincase, only the anterior part of the parasphenoid showing grooves for the internal carotid arteries and vidian nerves, and the long, narrow cultriform process are preserved. Associated with the cultriform process in both specimens of *Cochleosaurus florensis* are parts of the ossified sphenethmoid. It seems to be broadest in its middle portion but tapers anteriorly, barely reaching the vomers. The posterior part of the sphenethmoid is lacking. The parasphenoid articulates with large processes of the pterygoids. The right pterygoid of MCZ 4344 bears a notched process against which fitted the antero-lateral edge of the parasphenoid. The posterior parts of the braincase are lacking.

The palate of *C. florensis* shows four to five irregular longitudinal rows of small denticles on the palatine rami of the pterygoids. Each vomer bears several ridges, on each of which runs one row of small denticles. These ridges radiate from the vomerine fangs, three anteriorly, one transversely, and two posteriorly on each vomer. In *Caerorhachis* (Holmes and Carroll 1977) and in *Dendrerpeton* (Carroll 1967*a*), a shagreen of small denticles is evenly distributed over all palatal bones, a primitive condition. With reference to specimen MCZ 4343, the premaxilla of *Cochleosaurus florensis* bears thirteen or fourteen tooth positions, with seven teeth *in situ*. The maxilla shows thirty-six tooth positions with twenty-one teeth *in situ*. This results in a total of forty-nine or fifty teeth for each upper jaw ramus of *C. florensis*. Fritsch (1889) estimated a total of fifty teeth for each upper jaw ramus of *C. bohemicus*.

A lateral view of the left mandibular ramus is shown in MCZ 4343. A large angular extends far anteriorly. The posterior end of the lower jaw is formed by the surangular. The splenial and the postsplenial appear to be of about equal length, the splenial extending to the angular as in *Chenoprosopus* (Langston 1953). The suture between the splenial and the postsplenial in *Cochleosaurus florensis* (MCZ 4343) lies on a crack, and there is some suspicion that it may lie further anteriorly, which would result in a shorter splenial.

A tibia and a fibula as well as a clavicle can be identified, lying across the lower surface of the palate of *C. florensis* (MCZ 4343) (text-fig. 1). The association of these elements with *Cochleosaurus* is questionable. Other elongated elements may represent ribs.

DISCUSSION

Palaeogeography

During the Middle Pennsylvanian, the genus *Cochleosaurus* inhabited Europe (*C. bohemicus* Fritsch, 1885) and, as far as presently known, eastern North America (*C. florensis* n. sp.), the two populations being distinct at the specific level. According to Milner and Panchen (1973) and Panchen (1977), the locality near Florence lies on the European side of the Appalachian Mountain Chain of Laurasia. These authors believe that *Cochleosaurus* represents an aquatic animal which was unable to migrate across the Appalachian Mountains. However, on the basis of the absence of lateral-line canals on the dermal skull bones, *Cochleosaurus* could be interpreted as a predominantly terrestrial genus, and indeed *Cochleosaurus* might also occur at Linton, Ohio, on the North American side of the Appalachian Mountain Chain (Milner, cited in Panchen 1977). A terrestrial habit of *Cochleosaurus* would fit the character of the Florence locality, which otherwise yielded predominantly terrestrial reptiles (Carroll 1969; Reisz 1972).

Relationships

A typical feature of *Cochleosaurus* is a pattern of strong and subdued sculpturing of dermal skull bones, associated with the depression of certain areas in *C. florensis*. The two species of *Cochleosaurus* can readily be distinguished by zones of intensive growth (Bystrow 1935), resulting in elongated pits in the sculpturing of *C. bohemicus* which are lacking in *C. florensis*. This is, however, a matter of maturity.

Within the closely related edopoid genera *Dendrerpeton*, *Cochleosaurus* and *Chenoprosopus*, a successive lengthening of the snout is observed. Although the snout of *Cochleosaurus florensis* is slightly shorter than in *C. bohemicus*, the snout of the genus *Cochleosaurus* in general is longer than in *Dendrerpeton* but shorter than in *Chenoprosopus*. *Cochleosaurus* is also morphologically intermediate between *Dendrerpeton* and *Chenoprosopus* with respect to the size of the interpterygoid vacuities.

Chenoprosopus is considered to be more advanced than *Cochleosaurus* and possibly a descendant of the latter by Langston (1953), although he places the genus in a distinct family. Romer (1966) includes *Chenoprosopus* within the Cochleosauridae. Significant similarities between *Cochleosaurus* and *Chenoprosopus*, as noted by Langston (1953), include the size and the shape of the internal nostrils as well as of the interpterygoid vacuities and the loss of the parietal foramen in adult specimens of both genera. To this list of similarities between *Cochleosaurus* and *Chenoprosopus* may be added the depressed area with subdued sculpturing in the preorbital region of *Chenoprosopus* covering the lacrimal bone, as well as a similar depression lying between the external nares. A primitive feature of *Chenoprosopus* is the single occipital condyle. The vomers do not enter the interpterygoid vacuities but are excluded from them by the pterygoids which turn inwards to contact the tip of the cultriform process in an interdigitating suture. This might represent a secondary specialization of *Chenoprosopus* rather than a primitive feature.

Dendrerpeton resembles Cochleosaurus in the shape and position of the postorbital and temporal series of bones. The lacrimal bone broadly enters the orbit in *Dendrerpeton*, however, a primitive feature that has been lost in *Cochleosaurus*. The jugal does not enter the lower margin of the cheek in *Dendrerpeton* as it does in *Cochleosaurus*. The pineal foramen is persistently large in *Dendrerpeton*, another primitive feature of the genus. The palate of *Dendrerpeton* appears to be more primitive than the palate of *Cochleosaurus*. Denticles are found on all palatal bones of *Dendrerpeton*, while in *C. florensis* they are restricted to the pterygoids and vomers. The vomers of *Dendrerpeton* lack the ridges described above for *C. florensis*.

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DINOFLAGELLATE CYSTS AND ACRITARCHS FROM UPPER BAJOCIAN TO MIDDLE BATHONIAN STRATA OF CENTRAL AND SOUTHERN ENGLAND

by J. P. G. FENTON, R. NEVES, *and* K. M. PIEL

ABSTRACT. Ten samples for palynological analysis were collected from three localities, Hook Norton, Bruton, and Burton Bradstock, in central and southern England. All samples contained abundant Middle Jurassic microplankton and the following taxa are described as new: *Dichadogonyaulax adelos* sp. nov.; *Gongylodinium erymnoteichos* gen. et sp. nov.; *G. hocneratum* gen. et sp. nov.; *Kylindrocysta spinosa* gen. et sp. nov.; *Tenua asymmetra* sp. nov. *Caddasphaera halosa* gen. nov. comb. nov. and *Leptodinium pectinigerum* are proposed as new combinations. The stratigraphical significance of the assemblages is discussed.

As part of a wider investigation into the distribution of palynomorphs in the Middle Jurassic rocks of England, ten samples of Upper Bajocian to Middle Bathonian age were collected from three well-known localities that are dated by ammonites—Hook Norton, Oxfordshire; Bruton, Somerset; and Burton Bradstock, Dorset (text-fig. 1). The palynological assemblages recovered contain abundant, well-preserved, and diverse dinoflagellate cysts, acritarchs, and miospores. This paper is concerned with the two former categories, which include new taxa and are of stratigraphical value.

Slides containing the illustrated types and assemblage strew mounts are retained in the collection of the Micropalaeontology Laboratory, Department of Geology, University of Sheffield. All specimen locations on the slides are given by England Finder co-ordinates.

STRATIGRAPHICAL LOCATION OF SAMPLES

1. *Burton Bradstock, Dorset.* The oldest sample (BB5) was collected from the *Truellei* Bed of the Burton Limestone, which is exposed in the road cutting leading to the cliff top at Burton Bradstock (Grid Reference SY487889). A sample of blue/grey oolitic limestone was collected 0·3 m above the base of the bed, which is here 0·5 m thick, and has been attributed to the *S. truellei* Subzone of the *P. parkinsoni* Zone (Upper Bajocian) by Richardson (1928, p. 62) and Parsons (1974).

2. *Hook Norton, Oxfordshire.* The best exposure at Hook Norton is on the eastern side of the disused railway cutting, south of the tunnel entrance (SP367317, Duckpool Farm cutting of Walford 1883; see text-fig. 2). Samples HNRC 1–6 were collected from this section where the Upper Bajocian–Lower Bathonian rests unconformably upon Upper Liassic shales and clays (*H. bifrons* Zone; Howarth 1978, p. 247). Lithological correlation with the section documented from the north cutting by Richardson (1911) is fairly straightforward (text-fig. 1, loc. 2). About 2·1 m of Aalenian strata (belonging to the *L. opalinum* Zone) which are present in the north cutting are absent, as noted by Walford (1883, p. 243) and Horton (1977, fig. 2). These strata have been attributed to the *Scissum* Beds by Richardson (1911) and the Northampton Sand by Horton (1977), these terms applying to laterally equivalent strata.

The Upper Bajocian Hook Norton Conglomerate Beds (Beds 22–24 of Richardson 1911) are expanded in thickness from 0·5 m in the north cutting to 0·9 m in the south cutting, where they rest directly upon the Lias. Samples HNRC 1–3 are from these beds, a series of intercalated variegated oolitic muds and clays, bioclastic oolitic or even pisolitic microsparitic limestones with occasional lenses of homeolithic pebbly limestones. Both Richardson (1911) and Horton (1977) have correlated them lithologically with the *Clypeus* Grit, which has been assigned to the *P. bomfordi* Subzone of the *P. parkinsoni* Zone (Parsons 1976).

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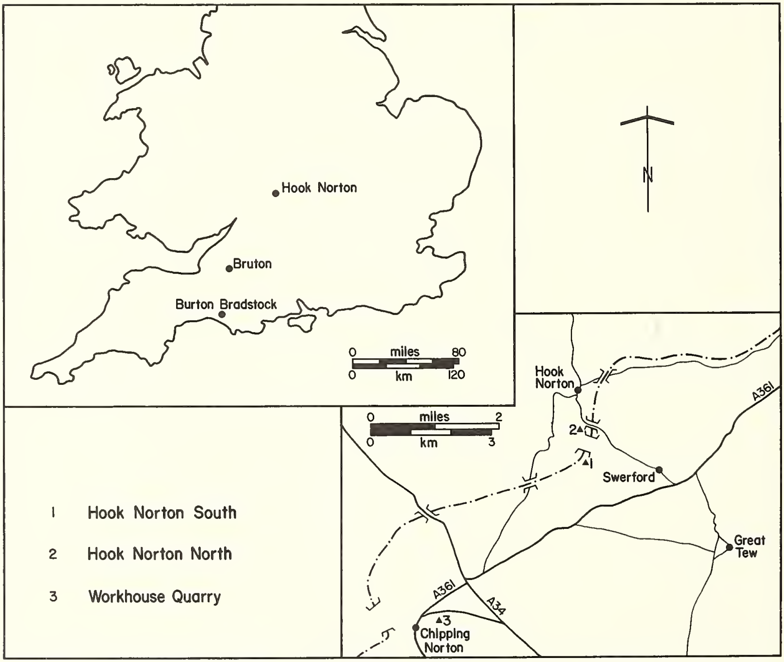
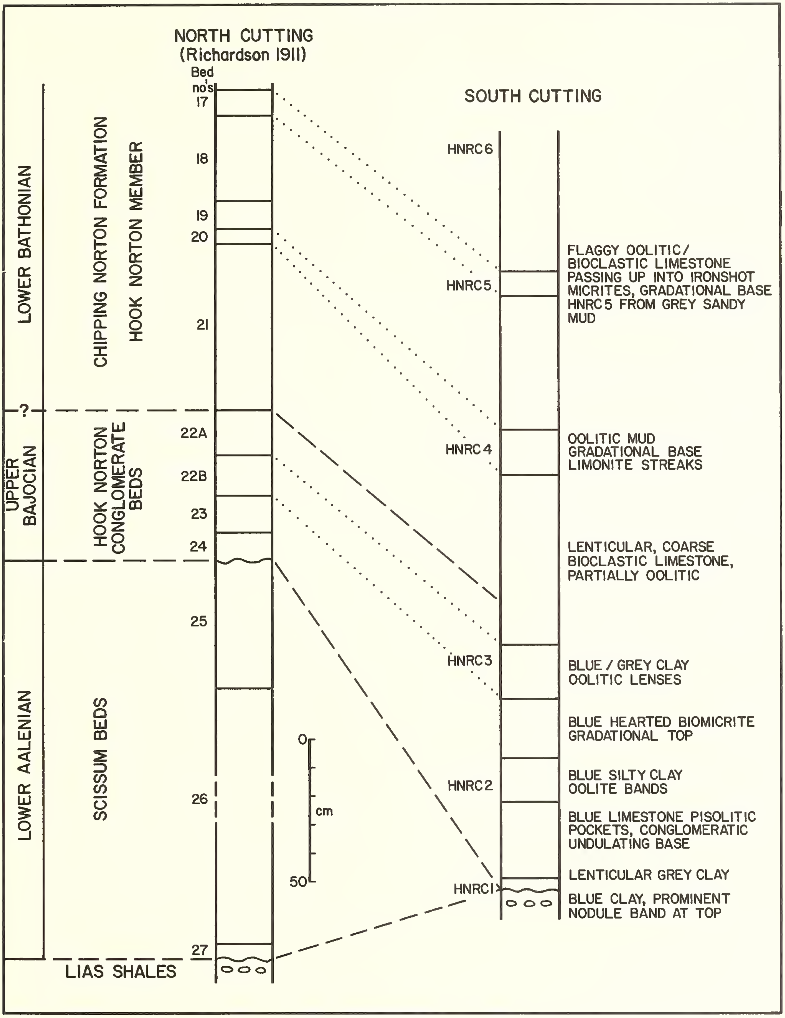
Samples HNRC 4–6 are from within the Hook Norton Member, a sequence of oolitic and bioclastic sandy limestones, oolitic sandy muds, and calcareous quartz sands, all rich in lignite. This Member forms the basal part of the Chipping Norton Formation, and the Bajocian–Bathonian boundary is thought to occur near its base (Torrens 1968, p. 228). The upper part of the Member is assigned to the *P. convergens* Subzone of the *Z. zigzag* Zone (Lower Bathonian) (Torrens 1968). At Workhouse Quarry, Chipping Norton (SP319276), approximately 3·5 km to the south-west (text-fig. 1, loc. 3) the boundary is thought to occur about 1 m below the *Trigonia signata* Bed (Parsons pers. comm. 1978). Richardson (1911) correlated the latter with Bed 12 ('The Old Man') of his account of the north cutting at Hook Norton. Detailed correlation of the section studied with that above Richardson's Bed 17 in the north cutting must remain tentative. However, if the Bajocian–Bathonian boundary occurs at approximately the same horizon below the *T. signata* Bed as supposed at Chipping Norton, it will be near the horizon of Beds 18 and 19 of Richardson (1911). Horton (1977, p. 151), however, states that no evidence has been found during the recent geological investigation of the Chipping Norton area (Geological Survey Sheet 218) to support the proposal of Walford and Richardson that the *T. signata* Bed is a discrete traceable horizon.

Sample HNRC 7, a pale-grey calcareous sandy clay, was taken 0·5 m above the base of the Conglomerate Beds, about 100 m south of the main section. Whilst it is thought to be stratigraphically equivalent to sample HNRC 2, the precise correlation is obscure due to poor exposure between the localities, compounded by lateral facies changes.



TEXT-FIG. 1. Geographical location of sample localities, inset showing further details of the Hook Norton locality.


NORTH CUTTING
(Richardson 1911)
Bed no's
17
18
19
20
21
22A
22B
23
24
25
26
27
LIAS SHALES
LOWER BATHONIAN
UPPER BAJOCIAN
LOWER AALENIAN
?
CHIPPING NORTON FORMATION
HOOK NORTON MEMBER
HOOK NORTON CONGLOMERATE BEDS
SCISSUM BEDS
0
cm
50
SOUTH CUTTING
HNRC6
HNRC5
HNRC4
HNRC3
HNRC2
HNRC1
FLAGGY OOLITIC/ BIOCLASTIC LIMESTONE PASSING UP INTO IRONSHOT MICRITES, GRADATIONAL BASE HNRC5 FROM GREY SANDY MUD
OOLITIC MUD GRADATIONAL BASE LIMONITE STREAKS
LENTICULAR, COARSE BIOCLASTIC LIMESTONE, PARTIALLY OOLITIC
BLUE / GREY CLAY OOLITIC LENSES
BLUE HEARTED BIOMICRITE GRADATIONAL TOP
BLUE SILTY CLAY OOLITE BANDS
BLUE LIMESTONE PISOLITIC POCKETS, CONGLOMERATIC UNDULATING BASE
LENTICULAR GREY CLAY
BLUE CLAY, PROMINENT NODULE BAND AT TOP

TEXT-FIG. 2. Correlation between the main section studied at Hook Norton and that of Richardson (1911).

Sample HNRC 8 was collected from a lignite-rich oolitic mud intercalated between massive bioclastic and oolitic limestones on the western side of the north cutting, about 50 m north of the tunnel entrance (SP359321; see text-fig. 1, loc. 2. It is considered to be stratigraphically higher than samples HNRC 1–7, occurring within the Hook Norton Member, and to be of Lower Bathonian age.

3. *Bruton, Somerset.* The locality at Bruton railway station (ST368847) was sampled in a temporary trench on the south side of the railway line. The sample (BRUT 1) of blue/grey silty mud containing abundant *Praexogyra acuminata* (J. Sowerby) was collected about 0·3 m below track level. Stratigraphically the sample is located within the *Acuminata* Beds, which are placed at the top of the Lower Fuller's Earth Clay. These beds have yielded ammonite faunas which underlie the *T. subcontractus* Zone and have been correlated with the upper part of the *P. progracilis* Zone of the Middle Bathonian (Torrens 1974).

PREVIOUS RESEARCH

Comparatively little has been published on the palynology of strata around the Bajocian–Bathonian boundary. The earliest papers are those of Valensi (1948, 1953), which were concerned with the Middle Jurassic microplankton from the Normandy and Poitiers regions of France. Despite the precise taxonomic investigation undertaken, scant attention was paid to stratigraphical distribution.

In 1966 W. Wetzel published a paper describing several new taxa from the *G. garantiana* Zone of Bielefeld, north-west Germany. In the same year Stover produced a short taxonomic paper describing a new species of *Nannoceratopsis* from the Lower Bathonian of Normandy. Unfortunately, little mention was made of the other microplankton elements within the assemblage. The publication of the classic Bathonian paper of Gocht (1970), whilst investigating the Lower Bathonian of some borehole cores in north-west Germany, described several new species and added a great deal to the understanding of dinoflagellate cyst ultrastructure.

Johnson and Hills (1973) published a palyno-stratigraphy of the Middle Jurassic Savik Formation from Arctic Canada. Unfortunately the assemblages round the Bajocian–Bathonian boundary were low in diversity and dominated by acritarchs and species of *Nannoceratopsis.* Van Helden (1977) also described assemblages from Arctic Canada, again dominated by the genus *Nannoceratopsis.* Fenton and Fisher (1978) give a brief description of microplankton in the Upper Bajocian–Lower Bathonian, within a broad account of Middle Jurassic (excluding the Callovian) microplankton ranges and geographical distribution in north-west Europe.

LIST OF TAXA CITED

DINOFLAGELLATE CYSTS:

A comprehensive bibliography of cited taxa is given by Lentin and Williams (1977).

Chytroeisphaeridia chytroeides (Sarjeant 1962) Downie and Sarjeant 1966; *C. dictydia* Sarjeant 1972; *C. pocockii* Sarjeant 1968; *Cleistosphaeridium polytrichum* (Valensi 1947) Davey *et al.* 1969; *Ctenidodinium combazii* Dupin 1968; *C. continuum* Gocht 1970; *C. ornatum* (Eisenack 1935) Deflandre 1938; *Dichadogonyaulax adelos* sp. nov.; *D. kettonensis* Sarjeant 1976*a*; *D. norrisii* (Pocock 1972) Sarjeant 1975; *D. sellwoodii* Sarjeant 1975; *D. stauromatos* Sarjeant 1976*a*; *Ellipsoidictyum cinctum* Klement 1960; *Gongylodinium erymnoteichos* gen. et sp. nov.; *G. hocneratum* gen. et sp. nov.; *Gonyaulacysta aldorfensis* Gocht 1970; *G. crispa* (W. Wetzel) Davey *et al.* 1969; *G. dangeardii* Sarjeant 1968; *G. eisenackii* (Deflandre 1938) Dodekova 1967; *G. filapicata* Gocht 1970; *G. jurassica* (Deflandre 1938) Norris and Sarjeant 1965; *Kalyptea glabra* (Cookson and Eisenack 1960) Wiggins 1975; *Kylindrocysta spinosa gen. et* sp. nov.; *Leptodinium pectinigerum* (Gocht 1970) stat. nov.; *L. regale* Gocht 1970; *Lithodinia callomonii* (Sarjeant 1972) Lentin and Williams 1977; *L. decapitata* (W. Wetzel 1966) Lentin and Williams 1977; *L. deflandrei* (Sarjeant 1968) Lentin and Williams 1977; *L. jurassica* Eisenack 1935; *L. valensii* (Sarjeant 1966) Lentin and Williams 1977; *Nannoceratopsis gracilis* Alberti 1961; *N. pellucida* Deflandre 1938; *N. spiculata* Stover 1966; *Pareodinia ceratophora* Deflandre 1947; *P. ceratophora* subsp. *scopeaus* (Sarjeant 1972) Lentin and Williams 1973; *Scriniodinium crystallinum* (Deflandre 1938) Klement 1960; *Tenua asymmetra* sp. nov.; *T. verrucosa* Sarjeant 1968; *Valensiella ampulla* Gocht 1970; *V. ovula* (Deflandre 1947) Eisenack 1963; *Wanaea acollaris* Dodekova 1975.

ACRITARCHS:

Caddasphaera halosa (Filatoff 1975) gen. nov. comb. nov.; *Cymatiosphaera eupeplos* (Valensi 1947) Deflandre 1954; *Micrhystridium fragile* Deflandre 1947; *M. stellatum* Deflandre 1942.

SYSTEMATIC PALYNOLOGY

Class DINOPHYCEAE Fritsch
Order PERIDINIALES Haekel
Family DICHADOGONYAULACEAE Sarjeant and Downie 1974
Genus DICHADOGONYAULAX Sarjeant 1966 emend. Sarjeant 1975

1966 *Dichadogonyaulax* Sarjeant *in* Davey *et al.*, p. 153.
1975 *Dichadogonyaulax* Sarjeant, 1966 emend. Sarjeant, p. 50.

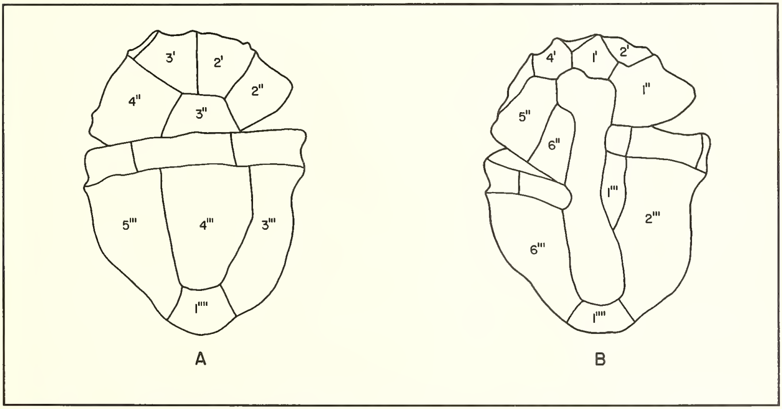
Type species. Dichadogonyaulax culmula (Norris 1965, p. 793, figs. 1, 2, 6–9) Loeblich Jr. and Loeblich III, 1968, p. 211.

Dichadogonyaulax adelos sp. nov.

Plate 14, figs. 1–4; text-fig. 3

1978 Dinoflagellate sp. A *in* Fenton and Fisher, pl. 1, fig. 7.

Diagnosis. Small proximate cyst, spheroidal to ovoidal outline, dorso-ventrally flattened. Lacking polar and median horns. Epicyst slightly smaller than hypocyst. Paracingulum relatively broad, strongly laevorotatory. Parasutures absent or indistinct, defined by simple lines, low rounded ridges, or rarely by alignment of low granules. Parasutures preferentially developed on epicyst. Paratabulation formula 4′, 6″, 6c, 6‴, 1⁗. Archaeopyle epicystal, schism occurring along the anterior margin of the paracingulum.



TEXT-FIG. 3. Camera lucida drawing of *Dichadogonyaulax adelos* sp. nov., holotype, showing paratabulation. A, dorsal view by transparency. B, ventral view. × *c*. 1260.

Description. The cyst possesses a ?double-layered wall, up to 1 μm thick. The epicyst is slightly smaller than the hypocyst, the latter appearing to be more rigid in construction than the epicyst which is prone to break up along the parasutures. Four apical paraplates occur, paraplate 1′ occupying an anterior prolongation of the parasulcus. Paraplates 2′–4′ are polygonal, with paraplate 4′ being slightly reduced in area. Six roughly trapezoidal precingular paraplates occur, with paraplate 3″ being reduced in area. Paraplate 6″ is reduced to an elongate shape adjacent to the anterior parasulcal area.

The paracingulum is relatively broad (3–5 μm), strongly laevorotatory and offset by about twice its width. It is subdivided into six paraplates, with paraplate 1c the smallest. The undivided parasulcus is long and extends almost the whole length of the ventral surface. An expansion in width of the anterior area creates the impression of an intercalary paraplate, but no confirmative evidence could be found. The width is approximately constant on the hypocyst.

Six postcingular paraplates are identified, with paraplate 1‴ being severely reduced becoming narrow and elongate. The remainder are approximately trapezoidal in outline. The antapex is made up of a single small, subquadrate paraplate.

The surface of the cyst varies from faint to coarsely scabrate, with the occasional development of low (< 1 μm) isolated granules. The granules, when present, are often aligned in rough approximation to the parasutures. The latter are normally indistinct and may be completely absent from the hypocyst. The parasutures are best developed as very low rounded ridges (< 1 μm) or lines along which the epicyst may break up. In all the specimens observed the epicyst remained attached to the hypocyst on the ventral surface after archaeopyle development.

Dimensions. Cyst width—26(30)37 μm (18 specimens measured), length—30(35)48 μm; holotype width—37 μm, length—48 μm.

Occurrence. HNRC 1, 2.

Holotype. Plate 14, fig. 3 and text-fig. 3. *Paratypes.* Plate 14, figs. 1, 2.

Type horizon. Sample HNRC 1, base of Hook Norton Conglomerate Beds, Hook Norton, Oxfordshire, England. *P. bomfordi* Subzone, *P. parkinsoni* Zone, Upper Bajocian.

Remarks. D. adelos differs from all other species of *Dichadogonyaulax* by its small size, paratabulation, and parasutural ornament. The paratabulation is very indistinct, only being fully resolved on the holotype. Its absence on the hypocyst gives *D. adelos* a superficial resemblance to the genus *Mancodinium* Morgenroth, 1970. However, the latter differs in possessing a more complex epicystal paratabulation and a non-tabulate hypocyst.

D. adelos has also been recorded from the *H. discites* and *W. laeviuscula* zones (Lower Bajocian) of eastern England (Fenton and Fisher 1978).

Derivation of name. Adelos, Greek—obscure; with reference to the indistinct paratabulation.

EXPLANATION OF PLATE 14

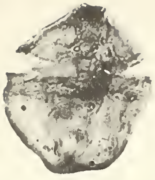
All magnifications × 1000.

Figs. 1–4. *Dichadogonyaulax adelos* sp. nov. 1, paratype, median view, HNRC 2ci (H43/4). 2, paratype, dorsal view, HNRC 2ci (V36/3). 3, holotype, ventral view, HNRC 1ci (L36/1). 4, dorsal view, HNRC 2ci (V37/4).

Fig. 5. *Caddasphaera halosa* comb. nov. HNRC 1ci (O29/4).

Figs. 6–9. *Gongylodinium erymnoteichos* gen. et sp. nov. 6, paratype, dorsal view, BB5 cii (R45/4). 7, ventral view, BB5 cii (M39/0). 8, holotype, dorsal view, HNRC 4cii (V39/4). 9, holotype, median view.

Figs. 10–13. *Kylindrocysta spinosa* gen. et sp. nov. 10, paratype, lateral view, HNRC 2ci (H43/4). 11, paratype, lateral view, HNRC 8ci (N46/0). 12, paratype, ventral view, HNRC 8ci (U46/0). 13, holotype, lateral view, BB5 ci (T50/1).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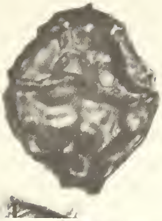
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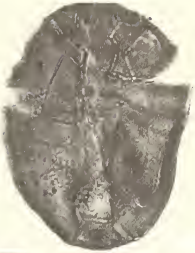
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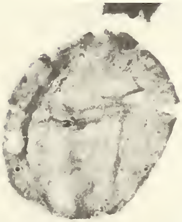
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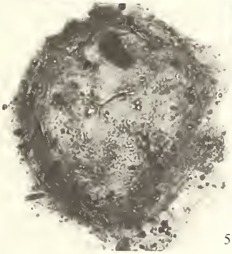
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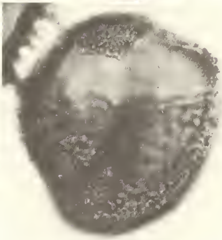
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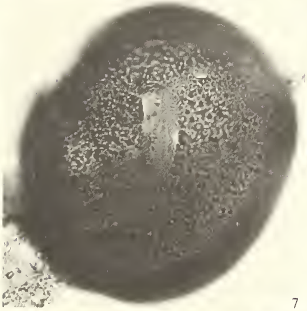
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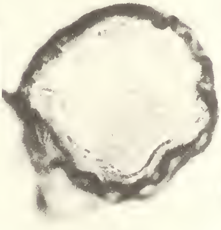
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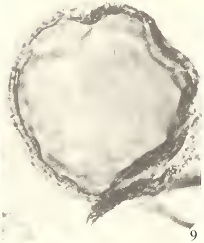
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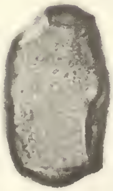
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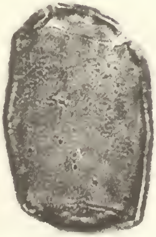
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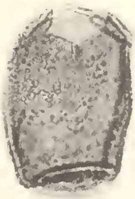
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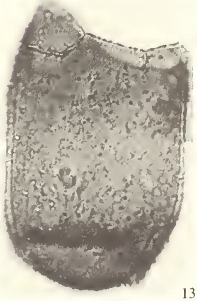
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FENTON, NEVES and PIEL, Jurassic microplankton

Family GONYAULACYSTACEAE Sarjeant and Downie, 1966

Genus LEPTODINIUM Klement, 1960 emend. Sarjeant, 1969

Type species. Leptodinium subtile Klement, 1960, p. 46, pl. 6, figs. 1–4, text-figs. 23, 24.

Leptodinium pectinigerum (Gocht, 1970) comb. nov.

1970 *Leptodinium subtile* subsp. *pectinigerum* Gocht, p. 138, pl. 33, figs. 1–4, text-fig. 11.

Remarks. The species is elevated from subspecific to specific rank, since we consider that it differs sufficiently from *L. subtile*. The major differences are the presence of a blunt, often conspicuous apical horn formed by the coalescing of the parasutural crests, and the highly denticulate to spinose parasutural crests. *L. subtile* lacks an apical horn and possesses unornamented parasutural crests.

The apical horn in *L. pectinigerum* is slightly displaced towards the ventral surface, as noted by Gocht (1970); the full paratabulation formula is: 4′, 6″, ?6c, 6‴, 1p, 1⁗, 1pv, 1ps.

Several specimens were observed with very finely perforate parasutural crests, but further specimens are required before a complete reappraisal of the species can be made.

L. pectinigerum has been recorded by Fenton and Fisher (1978) from the Upper Bajocian (*G. garantiana* Zone) to Upper Bathonian of north-west and south-west Germany. It has also been recorded by one of us (J. P. G. F.) from the Lower Callovian (*M. macrocephalus* Zone) of eastern England.

Family APTEODINIACEAE Eisenack, 1961 emend. Sarjeant and Downie, 1972

Genus GONGYLODINIUM gen. nov.

Type species. Gongylodinium erymnoteichos sp. nov.

Diagnosis. Proximate, non-tabulate cyst, spheroidal to ovoidal in outline. Paracingulum and parasulcus absent or very indistinct. Archaeopyle formed by loss of two trapezoidal paraplates in a dorsal precingular position. Thickness of wall variable. Ornament varying from smooth to scabrate to granulate or spinose, evenly distributed. Polar and median horns absent.

Remarks. Gongylodinium differs from all other genera in lacking polar and median horns and possessing a two-paraplate precingular archaeopyle. The genus bears a superficial resemblance to *Bitectatodinium* Wilson, 1973, described from the Middle Pleistocene of New Zealand, but differs in possessing larger opercular paraplates and a simpler non-tectate wall structure. It also differs from *Occisucysta* Gitmez, 1970 by lacking a definable paratabulation.

Derivation of name. Gongylos, Greek—round, spherical; with reference to the cyst shape of the type species.

Gongylodinium erymnoteichos sp. nov.

Plate 14, figs. 6–9

1965 *Leiosphaeridia scrobiculata* Deflandre and Cookson, 1955 *in* Dupin, pl. 2B, fig. 2.
1970 Gen. et sp. indet. 5 *in* Gocht, p. 153, pl. 34, fig. 28, text-fig. 27.
1978 Gen. et sp. indet. 5 *in* Fenton and Fisher, pl. 1, fig. 17.

Diagnosis. Proximate, non-tabulate cyst, spheroidal to slightly ovoidal outline. Paracingulum absent; parasulcus occasionally defined by reduction or absence of ornament. Archaeopyle formed by loss of two paraplates corresponding to a dorsal precingular position relative to the parasulcus. Double-layered wall thick, densely covered with squat spines, coni, and papillae.

Description. The normally spherical cyst is prone to collapse when the opercular paraplates are lost or have fallen inside the autocoel. Short accessory archaeopyle parasutures may occur, vaguely defining apical or ?paracingular paraplates. Occasionally a protrusion occurs at the mid-point of the anterior margin of the archaeopyle representing an anterior intercalary paraplate.

The wall is 1·5–2 μm thick and appears fairly homogeneous, with a dense cover of squat, blunt, or pointed spines, coni, or papillae. 0·5–1 μm high. The ornament may be absent or reduced on the depressed elongate parasulcal area which may be the location of preferential folding.

Dimensions. Cyst diameter—44(51)57 μm (15 specimens measured); holotype diameter—46 μm.

Occurrence. BB5, HNRC 4, 6.

Holotype. Plate 14, figs. 8, 9. *Paratype*. Plate 14, fig. 6.

Type horizon. Sample HNRC 4, Hook Norton Member, 0·7 m above the base, Chipping Norton Formation, Hook Norton, Oxfordshire, England. Upper Bajocian (*P. parkinsoni* Zone) or Lower Bathonian (*Z. zigzag* Zone).

Remarks. *G. erymnoteichos* is characterized by its thick wall and dense ornament cover. The archaeopyle is present in all specimens observed. The earliest record of the species is by Dupin (1965), who recorded it as *Leiosphaeridia scrobiculata*, from the Bajocian–Bathonian of the Aquitaine Basin, south-west France. A single specimen was recorded by Gocht (1970) as gen. et sp. indet. 5, and accords exactly with *G. erymnoteichos*. A single larger specimen (78 μm diameter) described as gen. et sp. indet 6 in the same paper is of questionable synonymy due to its larger size, although it appears very similar in over-all morphology. Both specimens were described from the Lower Bathonian of north-west Germany. Fenton and Fisher (1978) recorded specimens as gen. et sp. indet. 5 from the *P. parkinsoni* Zone (Upper Bajocian) to *O. aspidoides* Zone (Upper Bathonian) of south-west Germany and eastern England.

Derivation of name. *Erymnos*, Greek—fenced; *teichos*, Greek—wall; with reference to the castellated effect imparted by the ornamentation in section view.

Gongylodinium hocneratum sp. nov.

Plate 16, fig. 2

1970 Gen. et sp. indet. 4 *in* Gocht, p. 153, pl. 34, figs. 26, 27.

Diagnosis. Proximate, non-tabulate cyst, ovoidal or rarely spheroidal in outline. Paracingulum and parasulcus absent or indistinct. Archaeopyle precingular, by loss of two equidimensional dorsal precingular paraplates. Wall thin, smooth to scabrate.

Description. The cyst is normally ovoidal, rarely becoming spheroidal. The wall is thin, 1 μm or less, and varies from smooth to scabrate. The paracingulum and parasulcus are normally absent, but may occasionally be indicated on the ventral surface by a reduction in ornament or the presence of a shallow depression. The opercular paraplates are trapezoidal in outline, and during excystment may fall inside the autocoel. A small protrusion on the anterial archeopyle margin may indicate an intercalary paraplate. The frequent absence of this plate causes a small notch to be present on the anterior margin.

Dimensions. Cyst width—52(62)78 μm (17 specimens), length—53(62)73 μm; holotype width—61 μm, length—62 μm.

Occurrence. BB5, HNRC 1.

Holotype. Plate 16, fig. 2.

Type horizon. Sample HNRC 1, base of Hook Norton Conglomerate Beds, Hook Norton, Oxfordshire, England. *P. bomfordi* Subzone, *P. parkinsoni* Zone, Upper Bajocian.

Remarks. Although only two specimens were observed in this study, sufficient material has been described previously by Gocht (1970) and observed, and measured, by one of us (J. P. G. F.) from Lower Bathonian strata of south-west Germany, to justify the erection of this new species.

The anterior margin of the archaeopyle and opercular paraplates often appears irregular and ragged as if the two paraplates have been torn from the wall. In addition the loss of these paraplates during excystment frequently causes the epicyst to be distorted.

G. hocneratum differs from *G. erymnoteichos* in lacking strong ornament, having a thinner wall, and being more ovoidal in outline. The species has been observed by one of us (J. P. G. F.) in strata of Upper Bajocian (*G. garantiana* and *P. parkinsoni* zones) and Lower Bathonian (*Z. zigzag* Zone) age in north-west and south-west Germany. To date it has not been observed outside strata assigned to these three ammonite zones.

Derivation of name. Hocneratum, Anglo-Saxon name for the village of Hook Norton, first cited in A.D. 917.

Family CANNINGIACEAE Sarjeant and Downie, 1966 emend. Sarjeant and Downie, 1974

Genus TENUA Eisenack, 1958 emend. Sarjeant, 1968

1958 *Tenua* Eisenack, p. 410.
1968 *Tenua* Eisenack, 1958 emend. Sarjeant, p. 230.

Type species. Tenua hystrix Eisenack, 1958, p. 410, pl. 23, figs. 1–4, text-fig. 10.

Tenua asymmetra sp. nov.

Plate 16, figs. 1, 3, 5

Diagnosis. Proximate, non-tabulate cyst, rounded to ovoidal outline. Wall thin, ornamented with rugulae, granules, spines, baculae, and briefly bifurcate processes concentrated at the antapical pole, becoming reduced or absent towards the apex. Paracingulum and parasulcus absent or indistinct, defined by reduction or absence of ornament. Archaeopyle apical in development with accessory parasutures defining six precingular paraplates.

Description. The outline of the cyst is variable, as the thin wall ($< 0{\cdot}5\ \mu m$) is prone to breakage along the accessory archaeopyle parasutures. This feature exaggerates the width and facilitates easy folding of the cyst.

At the antapical pole the ornament consists of irregularly distributed rugulae, granules, blunt or pointed spines, baculae, and briefly bifurcate processes, all under 2 μm in height. The surface is coarsely scabrate, becoming faintly scabrate or occasionally smooth anterior to the coarsely ornamented antapex. The diverse ornamentation is also reduced in size and density anterior to the antapical pole. When the ornament is totally absent, often due to corrosion, the autophragm takes on an infra-vermiculate appearance. When present, the paracingulum varies between 3 and 6 μm in width.

Dimensions. Cyst width—60(74)94 μm (18 specimens measured), length—57(68)80 μm; holotype width—60 μm, length—58 μm.

Occurrence. BB5, HNRC 1, 4, 5, 8.

Holotype. Plate 16, fig. 3. *Paratype.* Plate 16, figs. 1, 5.

Type horizon. Sample BB5, *Truellei* Bed, Burton Bradstock, Dorset, England. *S. truellei* Subzone, *P. parkinsoni* Zone, Upper Bajocian.

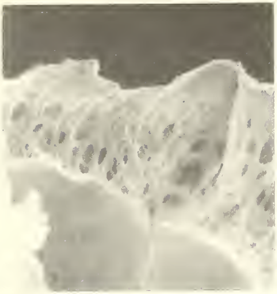
Remarks. T. asymmetra differs from all other species of *Tenua* by the possession of asymmetrically developed ornament of great diversity. The cyst width is very approximate due to the tendency of specimens to break up along precingular parasutures, giving exaggerated dimensions.

EXPLANATION OF PLATE 15

SEM Magnifications. Fig. 1 × 3000; figs. 2, 4 × *c.* 4000; figs. 5, 6 × *c.* 2000. All specimens fron HNRC 2.

Figs. 1, 3. *Lithodinia valensii* (Sarjeant 1966) Lentin and Williams 1977. 1, detail of parasutural crest. 3, same specimen, detail of ventral surface.

Figs. 2, 4–6. *Kylindrocysta spinosa* gen. et sp. nov. 2, detail of closely adpressed endo- and periphragm. 4, detail of fibrous, spinose periphragm. 5, same specimen as fig. 2, detail of ?dorsal surface. 6, same specimen as fig. 4, detail of ?ventral/lateral surface, oblique view.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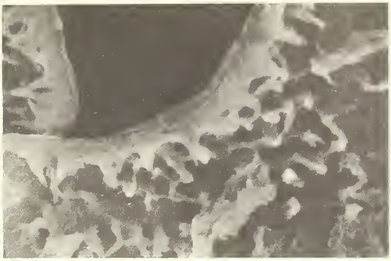
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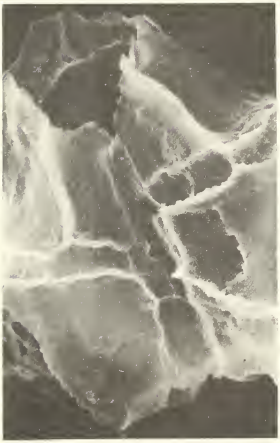
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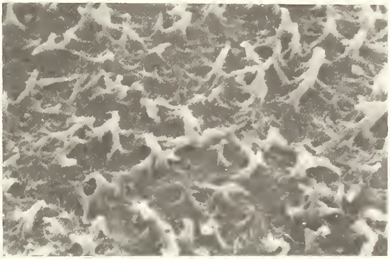
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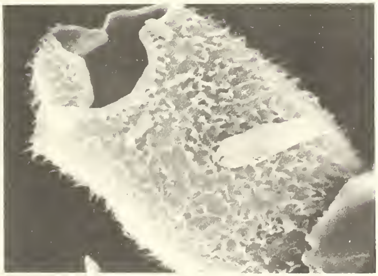
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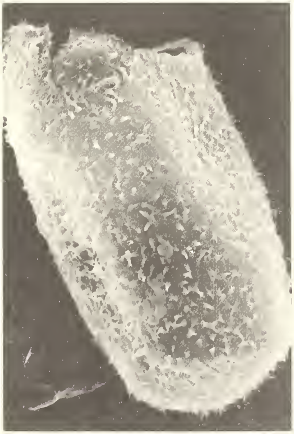

6

FENTON, NEVES and PIEL, Jurassic microplankton

The species bears a close resemblance to *Cyclonephelium* Deflandre and Cookson 1955 emend. Ioannides *et al.*, 1976. *T. asymmetra* differs, however, in lacking polar horns or protuberances and ornament restricted to a circumferential zone. However, the close similarity with *Cyclonephelium* makes *T. asymmetra* possibly related to the former genus.

When the ornament is developed at its best the species appears similar to *Chytroeisphaeridia pocockii* Sarjeant, 1968, although it differs by being larger and possessing an antapical polar concentration of ornament.

Derivation of name. Asymmetros, Greek—without symmetry; with reference to the distribution of ornament.

Family UNCERTAIN

Genus KYLINDROCYSTA gen. nov.

Diagnosis. Proximate cyst, cylindrical, strongly elongate to subquadrate in outline. Paratabulation absent or indistinct. Paracingulum and parasulcus apparently absent. Apex flattened or convex, composed of five paraplates, bulk of cyst composed of five elongate paraplates; with a flat to convex pentagonal antapical paraplate. Cyst wall complex, consisting of thin endophragm and spongy, fibrous periphragm, closely adpressed. Cyst surface spinose to granulose. Paratabulation formula 5′, ?5″, ?5‴, 1⁗. Archaeopyle formed by loss of two or more apical paraplates.

Type species. Kylindrocysta spinosa sp. nov.

Remarks. Kylindrocysta differs from all other genera by its shape, paratabulation formula, and type of archaeopyle. The closest comparable genus is *Pyxidiella* Cookson and Eisenack, 1958, but the latter differs in possessing a distinct intercalary archaeopyle and lacks a definable paratabulation.

Comparodinium Morbey, 1975 may possess a similar type of archaeopyle, in that it involves partial or total loss of the apical paraplates; it differs, however, in the possession of a distinct paracingulum and chorate structure to the cyst.

A similarity may be observed between *Kylindocysta* and *Pareodinia* Deflandre, 1947 emend. Wiggins, 1975 when partial loss of the apical paraplate series has occurred. *Kylindrocysta*, however, differs from *Pareodinia* in possessing a more angular shape, simpler paratabulation, more complex wall structure, and lacking an apical horn.

Kylindrocysta spinosa sp. nov.

Plate 14, figs. 10–13; Plate 15, figs. 2, 4–6

1970 *Pyxidiella* sp. *in* Gocht, p. 156, pl. 35, figs. 11, 12, text-figs. 28–30.

Diagnosis. Proximate cyst, cylindrical, elongate or subquadrate in outline. Cyst wall complex, consisting of thin endophragm and thicker fibrous periphragm, the latter bears a spinose ornament of medium to dense distribution. The apex consists of five apical paraplates, two ?dorsally inclined, subquadrate paraplates, and three smaller paraplates on the ?ventral surface. Archaeopyle formed by the loss of the two former paraplates or combination of all five paraplates. Remainder of cyst composed of five elongate to subquadrate paraplates and a single antapical paraplate. Paratabulation formula 5′, ?5″, ?5‴, 1⁗.

Description. Cyst normally elongate, cylindrical in shape, occasionally becoming more subquadrate in outline, due to the reduction in the length of the five elongate paraplates, which constitute the bulk of the cyst. The sides are straight to convex, never concave. The double-layered wall consists of a smooth, thin endophragm and a spongy, fibrous periphragm, the combined thickness varying between 1 and 2 μm. The periphragm appears fibrous with the individual fibres coalescing to form blunt or pointed, rarely capitate, spines, 0·5–2 μm high. The spines are medium to densely distributed over the entire cyst surface.

The apex consists of five paraplates. Two large subquadrate paraplates occur inclined towards the assumed dorsal surface and these are normally lost first in archaeopyle formation, but may remain attached to a diamond-shaped paraplate on the assumed ventral surface. Either side of this latter paraplate is one smaller trapezoidal to subquadrate paraplate.

Five long paraplates make up the bulk of the cyst, occasionally defined by accessory archaeopyle parasutures extending posteriorly from the apex or anteriorly from the antapex (when the antapical paraplate is displaced or lost).

Dimensions. Cyst width—22(28)33 μm, length—31(45)56 μm; holotype width—33 μm, length—54 μm (31 specimens measured).

Occurrence. BB5, HNRC 1–8.

Holotype. Plate 14, fig. 13. *Paratypes.* Plate 14, figs. 10–12.

Type horizon. Sample BB5, *Truellei* Bed, Burton Bradstock, Dorset, England. *S. truellei* Subzone, *P. parkinsoni* Zone, Upper Bajocian.

Remarks. The double-layered nature of the wall is only visible using SEM techniques, the wall appearing single layered under the light microscope. The parasutures are frequently observed best using transmitted light microscopy, often being unobserved with SEM techniques, possibly reflecting the fact that the parasutures are only developed on the thin endophragm.

The wall thickness of the holotype (Pl. 14, fig. 13) appears to be thinner than that of the paratypes, but this is due to slight corrosion of the fibrous periphragm. The specimen was selected to display the apical paraplate configuration of the cyst.

The nomenclature of the apical paraplates is debatable due to the lack of an obvious parasulcal area to use as a reference point. However, the diamond shaped paraplate to which the two largest apical paraplates are often attached is taken to lie upon the ventral surface and may correspond to a paraplate 1′ position. We favour the view that the two adjacent paraplates are probably additional apical but could be intercalary paraplates.

The paratabulation formula observed in this study is identical to that proposed by Gocht (1970, text-fig. 30).

K. spinosa appears to have a restricted stratigraphical range, being limited to the *P. parkinsoni* and *Z. zigzig* zones, having been previously recorded from the Lower Bathonian of north-west Germany (Gocht 1970) and the *P. parkinsoni–Z. zigzag* zones of north-west Europe (Fenton and Fisher 1978).

Derivation of name. Spinosus, Latin—thorny; with reference to the spinose ornament.

Dinoflagellate type 1

Plate 16, fig. 6

Description. Proximate, ?non-tabulate cyst, biconical in outline. Epi- and hypocyst of similar proportions. Cyst wall single layered (autophragm) thin, under 0·5 μm thick, scabrate. The conical epicyst has concave sides and is surmounted by a fairly broad, slightly rounded, hollow apical horn. Folds in the autophragm may correspond to the parasutures between the apical and precingular paraplate series. A large precingular archaeopyle is developed by the loss of one large elongate paraplate (3″). Parasulcus absent, paracingulum possibly defined by parallel folds, about 4 μm wide.

The hypocyst is extended into a distally closed, well-rounded antapical extension of the autocoel, with two folds possibly defining postcingular paraplates on the dorsal surface.

Dimensions. Cyst width—69 μm (single specimen only), length—110 μm.

Occurrence. BB5.

Remarks. Unfortunately only one well-preserved specimen of this highly distinctive cyst was observed, differing from all known genera by its shape, lack of paratabulation, cyst structure, and presence of a precingular archaeopyle. The specimen bears a superficial resemblance in outline to the genus *Tubotuberella* Vozzhennikova, 1967. The latter differs, however, in the possession of a distinct endophragm and an opisthopyle at the antapex.

Numerous specimens have been observed by one of us (R. N.) from strata assigned to a post-Aalenian–pre-Lower Kimmeridgian age from the northern North Sea Basin.

Dinoflagellate type 2

Plate 16, fig. 4

Description. Proximate, non-tabulate cyst, originally spherical, distorted due to folding. Cyst wall varying between 0·5 and 1 μm in thickness. Ornament ranges from coarsely scabrate to coarsely granular (< 1 μm high). Paracingulum absent, parasulcus possibly defined by reduction of ornament. Archaeopyle formed by the loss of three paraplates, equating with a precingular position relative to the parasulcus.

Dimensions. Cyst diameter—52–60 μm (2 specimens only).

Occurrence. HNCR 8.

Remarks. These specimens bear some resemblance to *Gongylodinium erymnoteichos* in over-all shape and construction, but differ in having smaller, less distinctive ornament and possessing a three-paraplate precingular archaeopyle. The latter feature is considered to be of sufficient significance as to preclude emplacement within *Gongylodinium*, which is restricted to cysts with a two-paraplate precingular archaeopyle.

Several specimens bearing a close resemblance to Dinoflagellate type 2 have been observed by one of us (J. P. G. F.) from the Middle-Upper Bathonian of eastern England.

Group ACRITARCHA Evitt, 1963
Subgroup SPHAEROMORPHITAE Downie, Evitt, and Sarjeant, 1963
Genus CADDASPHAERA gen. nov.

Diagnosis. Body hollow, spherical, wall thin. Surface smooth to coarsely granulate. Body surrounded by an irregular kalyptra. Excystment via a pylome, when observed.

Type species. Caddasphaera (ex *Kalyptea*) *halosa* (Filatoff, 1975) comb. nov. *in* Filatoff 1975, p. 91, pl. 29, figs. 10, 11.

Remarks. The genus is erected for simple spherical bodies with a variable ornament of acritarchous affinities, enveloped within an irregular kalyptra.

Derivation of name. Cadda, from the Cadda Formation; type locality of the type species. *Sphaera*, with reference to the body shape.

Caddasphaera halosa (Filatoff 1975) comb. nov.

Plate 14, fig. 5

1975 *Kalyptea halosa* Filatoff, p. 91; pl. 29, figs. 10, 11.

Holotype. Filatoff 1975, pl. 29, fig. 10.

Type locality. Dongara Borehole No. 5, 609·6 m, Cadda Formation, Western Australia, Lower Bajocian.

EXPLANATION OF PLATE 16

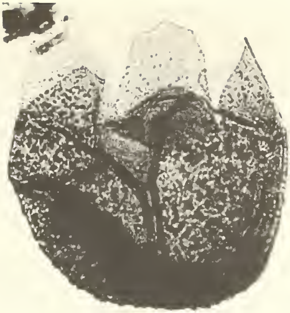
All magnifications ×1000, except fig. 6 ×750.

Figs. 1, 3, 5. *Tenua asymmetra* sp. nov. 1, paratype, median view, BB5 ciii, (P40/1). 3, holotype, ventral view, BB5 cii (O58/1). 5, paratype, dorsal view, BB5 cii (G63/3).

Fig. 2. *Gongylodinium hocneratum* gen. et sp. nov. Holotype dorsal view showing archaeopyle and opercula paraplates inside autocoel, HNRC lci (N40/4).

Fig. 4. Dinoflagellate type 2. Dorsal view showing incipient loss of three precingular paraplates, HNRC 8ci (U40/0).

Fig. 6. Dinoflagellate type 1. Dorsal view showing archaeopyle, BB5 cii (J67/0).



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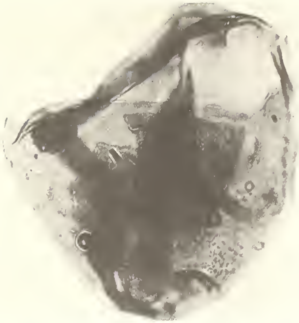

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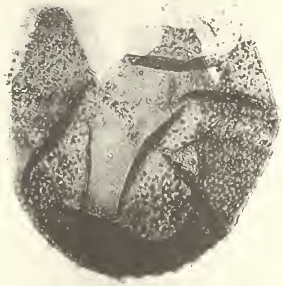

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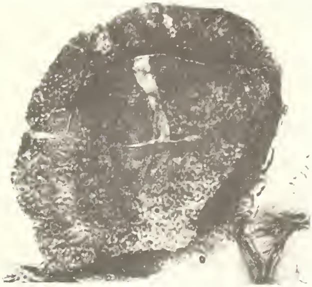

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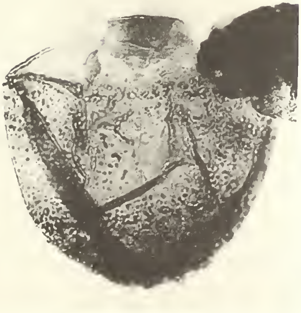

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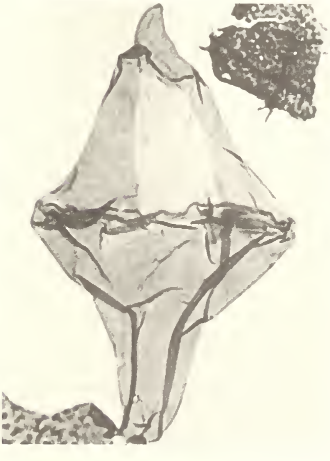

6

FENTON, NEVES and PIEL, Jurassic microplankton

Diagnosis. See Filatoff 1975, p. 91.

Remarks. Filatoff inappropriately placed this distinctive species in the dinoflagellate genus *Kalyptea* Cookson and Eisenack, 1960 emend. Wiggins, 1975, a genus possessing an intercalary archaeopyle and an apical horn ± an antapical horn. This species possesses neither an archaeopyle nor polar horns and is therefore more akin to the acritarchs. The enveloping kalyptra varies greatly in width, but it is always present around the body.

C. halosa (Filatoff, 1975) has been recorded from the Upper Liassic to Albian strata of eastern England (J. P. G. F. pers. obs.).

PALAEOGEOGRAPHY AND PALYNOSTRATIGRAPHY

The assemblages recorded are important for two main reasons. Firstly they offer conclusive microfloral evidence for the absence of Scissum Beds/Northampton Sand in the southern cutting at Hook Norton and thus support the observations of Walford (1883) and Horton (1977). Secondly, they are the first detailed assemblages to be recorded from Upper Bajocian and Lower to Middle Bathonian strata.

The absence of Aalenian strata variously assigned to the Scissum Beds or Northampton Sand is of palaeogeographical interest. Observations of microplankton assemblages from the Scissum Beds and Northampton Sand in Gloucestershire and Northamptonshire respectively, indicate that only nine of the thirty-four species encountered in samples HNRC 1-3, 7 extend into Aalenian strata (J. P. G. F. pers. obs.). The majority of the remaining twenty-five species make their first appearance in the Upper Bajocian. Assemblages recovered from the Scissum Beds and Northampton Sand are very similar to those recorded by Gocht (1964) from south-west Germany, and by Fenton and Fisher (1978) from north-west Europe. Therefore no doubt can be placed upon the Upper Bajocian age assigned to samples HNRC 1-3, 7.

Arkell (1933, p. 210) drew the Scissum Line extending approximately 50 km in a south-west/north-east direction through north Oxfordshire, into east Northamptonshire. To the south-east of the Scissum Line the Scissum Beds and the laterally equivalent Northampton Sand are overstepped by Upper Bajocian or younger strata. Arkell originally drew a more or less straight Scissum Line passing south of Swerford, which lies approximately 1 km to the south-east of Hook Norton south cutting. Horton (1977), on the basis of detailed field mapping and borehole evidence partially revises the Scissum Line (renamed Limit of Northampton Sand and Limit of Scissum Beds pockets) by drawing it in the vicinity of south cutting at Hook Norton (Horton 1977, fig. 4). Approximately 2·1 m of Aalenian strata (Scissum Beds) are overstepped by the Upper Bajocian within about 0·5 km between the north and south cuttings at Hook Norton.

In an area with relatively rare macrofaunal evidence for age determination, the presence of richly palyniferous horizons may be of use in determining a more precise stratigraphy and subsequently a more correct palaeogeography. In Oxfordshire and Northamptonshire, where a major stratigraphical hiatus separates Upper Bajocian and younger strata from Aalenian or older strata, the study of microplankton assemblages may be a readily applicable tool as differentiation between Aalenian and Upper Bajocian or younger assemblages is normally very easy.

From the stratigraphical aspect the assemblages appear fairly homogeneous, with key species being few in number and rare components of the assemblages (Table 1). The close similarity between Upper Bajocian and Lower Bathonian assemblages has been noted by Fenton and Fisher (1978). All the samples are rich in cysts with epicystal archaeopyles. The Bruton and Burton Bradstock samples have *Ctenidodinium* as the most abundant genus, whilst the Hook Norton samples are dominated by species of *Lithodinia* and *Dichadogonyaulax*, especially *D. stauromatos*.

Of the species recorded, *G. hocneratum*, *Nannoceratopsis gracilis*, *L. valensii*, and *Kylindrocysta spinosa* do not occur in strata younger than Lower Bathonian, whilst *D. adelos* and *Gonyaulacysta crispa* do not appear, at present, to extend stratigraphically higher than the Upper Bajocian (*P. parkinsoni* Zone). The remaining species which are here restricted to the Upper Bajocian: *D. norrisii*, *G.* cf. *dangeardii*, *Valensiella ampulla*, and *Cleistosphaeridium polytrichum* all range into

TABLE 1. Stratigraphical distribution of microplankton. O is recorded occurrence during present investigation; -O- known ranging into older and/or younger strata.

	BB	HNRC								BRUT
	5	1	2	7	3	4	5	6	8	1
Dinoflagellate type 1	O									
Dichadogonyaulax norrisii	-O-									
Gonyaulacysta cf. dangeardii	O-									
Cleistosphaeridium polytrichum	O-									
Gongylodinium hocneratum	-O	O								
Nannoceratopsis gracilis	-O	O								
Leptodinium pectinigerum	-O	O-			O		O-			
Lithodinia valensii	-O	O	O		O	O	O	O		
L. jurassica	O	O	O	O	O	O	O	O-		
Dichadogonyaulax sellwoodii	O		O		O	O	O	O	O-	
D. stauromatos	O	O	O	O	O	O	O		O-	
Ellipsoidictyum cinctum	O		O						O-	
Tenua asymmetra	O	O				O	O		O	
Nannoceratopsis pellucida	O							O	O-	
Gongylodinium erymnoteichos	-O					O			O-	
Leptodinium regale	-O	O	O			O			O-	
Lithodinia cf. deflandrei	-O	O	O		O	O	O	O	O-	
Kylindrocysta spinosa	O	O	O		O	O	O	O	O	
Chytroeisphaeridia pocockii	-O		O	O				O	O-	
Ctenidodinium combazii	O									O-
C. continuum	O		O		O					O-
C. ornatum	-O								O	O-
Gonyaulacysta aldorfensis	-O	O	O			O			O	O-
G. filapicata	-O	O		O			O			O-
Nannoceratopsis spiculata	-O		O			O	O	O	O	O-
Micrhystridium stellatum	-O		O		O	O	O	O	O	O-
M. fragile	-O	O	O			O	O		O	O-
Wanaea acollaris	O	O							O	O-
Pareodinia ceratophora	-O	O	O	O	O	O	O	O	O	O-
Dichadogonyaulax kettonensis	O	O	O		O	O	O	O	O	O-
Chytroeisphaeridia chytroeides	-O	O	O	O	O	O	O	O	O	O-
Valensiella ovula	-O	O	O		O	O	O	O	O	O-
Gonyaulacysta crispa		-O								
Valensiella ampulla		O	O-							
Dichadogonyaulax adelos		-O	O							
Caddasphaera halosa		-O	O	O	O	O	O	O-		
Chytroeisphaeridia dictydia		O							O-	
Kalyptea glabra		-O	O-							
Lithodinia decapitata/callomonii		O	O	O	O		O		O	O-
Gonyaulacysta eisenackii			O			O	O			O-
Scriniodinium cf. crystallinum					O-					
P. ceratophora subsp. scopaeus					O	O-				
Cymatiosphaera eupeplos						-O-				
Gonyaulacysta jurassica						O-				
Tenua verrucosa						O			O	O-
Dinoflagellate type 2									O-	
	TRUELLEI BED	H. NORTON CONG. BEDS				H. NORTON MEMBER				ACUMINATA BED
	BAJOCIAN					BATHONIAN				

younger strata in other geographical areas. The stratigraphical usefulness of Dinoflagellate type 1 and Dinoflagellate type 2 has yet to be evaluated.

For the purpose of defining the Bajocian–Bathonian boundary five species are thought to be of use. *D. adelos* and *G. crispa* are not known above the Upper Bajocian, whilst *G. jurassica*, *Scriniodinium* cf. *crystallinum* and *Tenua verrucosa* all appear, almost coincidentally, with the base of the Chipping Norton Formation. The effect of facies control upon the cyst assemblage is unknown, but little change occurs within the remainder of the assemblages spanning the formational boundary. Therefore, using palynological criteria to define the Bajocian–Bathonian boundary it appears that it may be drawn between samples HNRC 3 and 4, which equates approximately with the base of the Chipping Norton Formation. This is slightly lower than the extrapolated boundary from Chipping Norton Workhouse Quarry, assuming the *T. signata* Bed to be a synchronous deposit, although Horton (1977) states that no evidence can be found to support this.

The provincialism of dinoflagellate cysts, noted by Fenton and Fisher (1978) in the Upper Bathonian, may have been in existence at this earlier period. In their discussion they identify a Tethyan realm (southern Europe) and a Boreal realm (Greenland and Arctic Canada). The former has microplankton assemblages dominated by species of *Ctenidodinium*, especially *C. combazii*, whilst the latter is dominated by proximate cysts and is, in general, lacking cysts with epicystal archaeopyles. Eastern England is shown to possess a Boreal-type assemblage with the addition of species of *Dichadogonyaulax*. Oxfordshire is shown to be an area of mixing of this assemblage type with the *Ctenidodinium* dominated Tethyan assemblage.

Reference to Table 1 shows that *C. combazii*, although recorded at the top and bottom of the composite section studied, is only present in the more southern localities, at Burton Bradstock and Bruton. When species of *Ctenidodinium* (*C. continuum*, *C. ornatum*) are present in the Hook Norton assemblages they are heavily outnumbered by specimens attributable to various species of *Dichadogonyaulax* (*D. kettonensis*, *D. adelos*, *D. stauromatos*, and *D. sellwoodii*), which is the dominant genus in assemblages HNRC 1–8. The Upper Bajocian assemblage from Burton Bradstock (Dorset) contains approximately equal proportions of species of *Dichadogonyaulax* and *Ctenidodinium*, whereas the Upper Bathonian of Dorset contains a marked paucity of *Dichadogonyaulax* (Fenton and Fisher 1978). Assemblages from the Upper Bajocian (*P. parkinsoni* Zone) and Lower Bathonian (*Z. zigzag* Zone) of south-west Germany, and south-west and northern France contain a predominance of *Ctenidodinium* species, especially *C. combazii*, suggesting Tethyan realm affinities. The assemblage from Burton Bradstock exhibits a mixed Boreal/Tethyan microplankton content similar to those obtained from Oxfordshire in the Upper Bathonian. To explain this, assuming that facies control upon the cyst assemblages is negligible, it is suggested that waters containing abundant *Ctenidodinium* cyst producing motile dinoflagellate thecae transgressed northwards during the Lower Bathonian–Lower Callovian, moving the intermediary zone of mixing of assemblage types from Dorset in the Upper Bajocian to Oxfordshire and eastern England in the Upper Bathonian, eventually reaching the Moray Firth area (north-east Scotland) during the Lower Callovian (L. A. Riley pers. comm.).

CONCLUSIONS

Study of large assemblages of microplankton from samples spanning the Bajocian–Bathonian boundary show few diagnostic changes. It is thought that the youngest occurrence of *D. adelos* and *G. crispa* associated with the first occurrences of *G. jurassica*, *S.* cf. *crystallinum* and *T. verrucosa* may indicate the proximity of the Bajocian–Bathonian boundary.

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EXOSKELETON, MOULT STAGE, APPENDAGE MORPHOLOGY, AND HABITS OF THE MIDDLE CAMBRIAN TRILOBITE *OLENOIDES SERRATUS*

by H. B. WHITTINGTON

ABSTRACT. The external surface and morphology of the exoskeleton of *Olenoides serratus* is described; the exoskeletal layer has been replaced by illite and chlorite. The pleura curves down distally, there is no fulcral process or socket, but a flange assists in articulation. An early moult stage has the exoskeleton unmineralized and wrinkled, and was described as *Nathorstia transitans*. The type is redescribed; a second specimen is of the exoskeleton only. A new reconstruction of the biramous appendage is given. The outer branch was attached to the coxa so that it was extended close below the ventral cuticle of the body; the function was probably respiratory. The inner and ventral surfaces of the coxa, and the ventral side of the outer branch, were spinose. These limbs were adapted to sieze soft prey, squeeze, and shred it, and pass it forward to the mouth; a manner in which these activities could have been effected is outlined. The probable musculature of the limbs and a possible gait are described; this gait is unlike other modes of progression in trilobites that have been proposed. How *O. serratus* may have jumped off the bottom and drifted is suggested, the swimming powers were probably feeble, it could have ploughed shallowly in soft sediment. By alternate flexure and extension of pairs of limbs it could have dug in search of prey or for concealment; a *Rusophycus* type of trace may have resulted from such activity. *O. serratus* is thus considered to have been a benthonic predator and scavenger. No plausible limb movements by which it could have made a *Cruziana*-like trace are evident; how this trace was made is an unsolved problem.

THE earlier description of appendage-bearing specimens of *Olenoides serratus* (Whittington 1975) included a new reconstruction of the animal and a brief discussion of habits. Here additional details of exoskeletal composition and morphology are given, including those of unusual articulating devices in the thorax. The rare early moult stage ('*Nathorstia transitans*') is also redescribed. Further preparation, new photographs, and drawings have enabled a more detailed restoration of the biramous appendage. The limbs of *O. serratus* are now better known than those of any other species, and the basic limb movements here portrayed are those regarded as plausible by Manton (1977, pp. 39–53). Certain of these activities produce characteristic trackways. Studies of trace fossils attributed to trilobites (Bergström 1973; Birkenmajer and Bruton 1971; Campbell 1975; Crimes 1970, 1975; Martinsson 1965; Osgood 1970, 1975; Seilacher 1955, 1959, 1962, 1970) are largely concerned not with such relatively simple tracks but other and more complicated ones. These trace fossils have had to be interpreted in the absence of any incontrovertible evidence as to what animal made them, but suggestions have been derived from them of the behaviour and limb movements of trilobites. Certain of these suggestions are examined here with reference to *O. serratus*, and against the background of Manton's work. In *O. serratus* it appears that the filaments of the outer branch of the appendage cannot have been used in excavating or brushing away sediment, i.e. cannot have produced the fine scratches attributed to such an activity. Much attention has been devoted to the trace fossils *Rusophycus* and *Cruziana*. It appears plausible (text-fig. 14) that *O. serratus* could have made the former type of trace. On the other hand, no plausible solution has been advanced for the problem of by what limb movements was the trace fossil *Cruziana* made. I cannot devise one, and can see no plausible activity of *O. serratus* that would have resulted in this type of trace. No attempt is made here to re-assess any trace fossil. The suggestions made do, however, call into question interpretations of trace fossils that have gained some acceptance; greater caution is needed in such

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interpretations. *O serratus* belongs to a relatively small Middle Cambrian group that had few thoracic segments and the cephalon and pygidium are of similar size. Caution must likewise be used in drawing generalizations from this single species.

LOCALITY AND STRATIGRAPHICAL HORIZON

Specimens referred to herein came from C. D. Walcott's 'Phyllopod bed' in the quarry that he opened in 1910 for collecting from the Burgess Shale. This quarry is situated on the ridge between Wapta Mountain and Mount Field, at an elevation of approximately 2286 m (7500 ft), 4·8 km (3 miles) north of Field, southern British Columbia, Canada. Fritz (1971) described the geological setting of the Shale, and showed that the quarry was within the *Pagetia bootes* faunule of the *Bathyuriscus–Elrathina* Zone of the early Middle Cambrian. The Phyllopod bed is 2·3 m (7 ft 7 in.) thick, but the exact horizon from which Walcott's specimens came is not known. Parties led by the Geological Survey of Canada collected from the quarry in 1966 and 1967, and measured the levels within the Phyllopod bed from which their specimens were collected (Whittington 1971). In the explanations of the plates herein, specimens collected by Walcott, now in the U.S. National Museum, are recorded as from the Phyllopod bed. The level within this bed from which the Geological Survey of Canada's specimens came is given. Details of other specimens and their occurrence are in Whittington 1975, pp. 101–102, fig. 1.

METHODS AND SYMBOLS

Photographs. Those showing the exoskeleton (Pl. 17, figs. 1, 2; Pl. 18, figs. 1–3) have been taken using normal north-west lighting (north at the top of the plate), the specimen lightly coated with ammonium chloride sublimate. All other photographs were made on panchromatic film in ultraviolet radiation, after focusing in ordinary light. In some (Pl. 19, figs. 3, 4; Pl. 20, figs. 1, 3; Pl. 22, fig. 1) the radiation was directed at about 30° to the horizontal, the direction varied to bring out particular features. The direction is given in each explanation. In the remainder the radiation was directed at about 65° to the horizontal, and the specimen tilted to about 12°; this gives maximum reflection from the surface of the specimen. In all except Plate 22, fig. 3 (referred to as 'reflected'), the specimen was covered with a thin film of distilled water beneath a glass slip. The effect is to enhance definition and contrast between matrix and specimen; these photographs are referred to as 'under water'. The part of a specimen is taken to be that which shows the animal in dorsal aspect; photographs of a counterpart only are so specified in the explanations.

Text-figures. Two of the text-figures which explain my interpretation of the specimen are referred to as composite because they combine in one drawing, features shown by part and/or counterpart. Symbols used in the text-figures are as follows:

A, axis of promotor–remotor swing of coxa; ahr, articulating half-ring; am, anterior margin; an, antenna; ap, appendage; ax, axial ring; cb, coxa–body junction; ce, cercus; cox, coxa; d, depressor muscle; dl, distal lobe of gill branch; do, doublure; ex, dorsal exoskeleton; f, flexor muscle; fl, flange; fo, fold; g, suffix indicating gill (outer) branch; gn, gnathobase; gs, genal spine; G.S.C., Geological Survey of Canada; h, hinge joint; in, infilling; im, inner margin; iplf, interpleural furrow; is, inner surface; L, as prefix denoting left side of animal; le, levator muscle; ls, lateral spines; m, mould of exoskeleton; ma, margin; os, outer surface; p, pivot joint; pl, pleura; plf, pleural furrow; pls, pleural spine; py, pygidium, segments numbered 1py, 2py, etc.; pys, border spine of pygidium; pxl, proximal lobe of outer branch; R, as prefix denoting right side of animal; t, thorax, seven segments numbered 1t, 2t, etc.; U.S.N.M., United States National Museum (now National Museum of Natural History); v, ventral; ve, vein in rock; x, axis of articulation in thorax.

1–15, Arabic numerals used to denote successive thoracic segments, axial rings of pygidium, pleural furrows, podomeres of leg branch, etc. Also used to denote series of biramous appendages beginning with the most anterior shown by the specimen, when it was not the most anterior in the animal.

I–XV, Roman numerals used to denote successive biramous appendages in a series, beginning with the most anterior in relation to the animal, *not* the specimen.

Hachures represent minute scarps in the specimens, produced when the rock was originally split, or by preparation. The line runs along the upper edge of the scarp, the hachures directed down slope from this line. The scarps run along the broken edges of fragments of the exoskeletal layer, and at the changes in level which separate parts of the body. In the drawings they indicate the relative level of one part of the body to another.

Stipple indicates the position of ridges and furrows, other uses of stipple are explained individually.

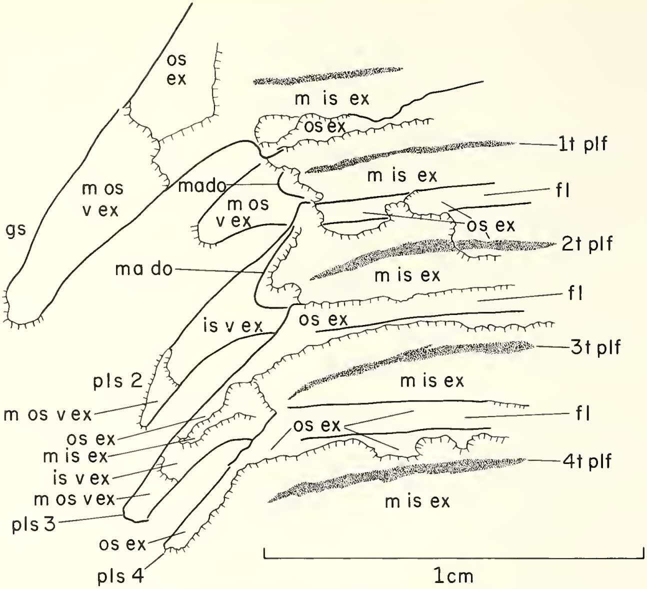
EXOSKELETON

The outer surface of the exoskeletal layer preserves in detail the original form (Pl. 17, fig. 1; Pl. 18, figs. 1–4). Granulation is coarsest on the posterior half of the axial rings, on the glabella and cheeks, and on the pleural ribs of thorax and pygidium; furrows are finely granulate to smooth. At the cephalic borders, and borders and spines of thorax and pygidium, the granulation grades into raised cusps which distally merge to form raised lines (Pl. 18, figs. 1, 4). On the anterior slope of the glabella and hypostome similar lines are formed (Whittington 1975, fig. 18, pl. 15, figs. 1–3). The steep scarp edges of the cusps face inwards, and so are opposed along the edges of the spines. On the ventral side of the spines and along the pygidial doublure are raised, anastomosing lines subparallel to the margin. The inner surface of the exoskeleton was smooth, as shown by the mould where the exoskeletal layer has been stripped off.

The broken edge of the exoskeletal layer (visible for example where it descends vertically into the doublure, Pl. 18, fig. 2, ex) appears black and shiny. A thin section was made across the posterior pygidial border of G.S.C. 61375, Walcott Quarry, level 6 ft 7·5 in. to 7 ft 3 in., an incomplete specimen showing portions of appendages. The exoskeletal layer is composed of minute flakes of a mineral, the flakes approximately at right angles to the surface. Electron microprobe analysis of the layer showed the presence of two distinct phases, an outer of illite (per cent by weight, MgO 4·85, Al_2O_3 31·32, SiO_2 37·20, S 0·18, K_2O 5·19, CaO 0·15, FeO 13·93, total 92·82, minus water), and an inner of chlorite (per cent by weight, MgO 9·93, Al_2O_3 24·08, SiO_2 25·51, S 0·08, K_2O 0·67, CaO 0·15, FeO 27·56, total 87·98, minus water). A fragment of the exoskeletal layer removed from G.S.C. 61374 (Pl. 18, fig. 3), gave the X-ray powder diffraction pattern of illite. It is assumed that the exoskeleton was originally mineralized with calcium carbonate, then replacement by illite group minerals occurred at some stage in diagenesis, perhaps at an early stage in an anoxic environment. Analyses quoted by Conway Morris (1977, p. 5) indicate that the soft parts of a fossil worm from the Burgess Shale are preserved in a film composed of calcium aluminosilicates, formed at some stage in diagenesis. Piper (1972, p. 173) remarked on the presence of diagenetic chlorite in portions of the Burgess Shale.

ARTICULATION OF THE THORAX

The earlier description of G.S.C. 34694 (Whittington 1975, pp. 119–120, pl. 20, figs. 1, 2, 4; pl. 21, figs. 1, 2; text-fig. 22) was primarily concerned with the appendages. Further preparation has revealed more completely the cheek (Pl. 18, fig. 4), and also the structure of the thoracic segments, including the articulating flange briefly alluded to earlier (Whittington 1975, p. 129). The flange fitted below the posterior pleural band of the segment in front, that of the first thoracic segment below the posterior border of the cephalon. Where the outer surface of the dorsal exoskeleton, or the mould of the inner surface, is not broken, the flange is concealed (e.g. right side of pleurae 5 to 7, Pl. 18, fig. 3; Whittington 1975, pl. 1, fig. 2; pl. 9, fig. 1). In 34694 the outer surface of the flange is exposed by the split or by preparation (Pl. 17, fig. 1; text-fig. 1; Pl. 18, fig. 2; text-fig. 2). The mould of the inner surface of the exoskeleton of the pleura, where exposed, lies only slightly above the outer surface of the exoskeleton of the succeeding flange, so that the two surfaces may in places appear to pass one into the other; in other places the slight difference in level is clear. The posterior margin of each flange is delineated by a narrow groove, and the flange is granulate. The flanges of the pygidium and seventh thoracic segment have been completely exposed by excavation (Pl. 18, fig. 2), in more anterior segments the flange is partially covered by the posterior pleural band. The abaxial margin is directed inwards and forwards, making a slight angle with the outer edge of the pleural spine. The flange is widest (exs.) abaxially, slightly narrower over most of its extent, proximally narrowing progressively as it curves down into the axial furrow. In the base of this furrow it merges into the outermost portion of the articulating half-ring. The ventral exoskeleton of the pleural spine extends inwards to form a band along the abaxial edge of the pleura, which narrows forwards and dies out, and does not extend under the flange. Postero-laterally the inner



TEXT-FIG. 1. Explanatory drawing of posterior portion of cheek lobe and pleural regions of first four thoracic segments in original of Plate 17, fig. 1.

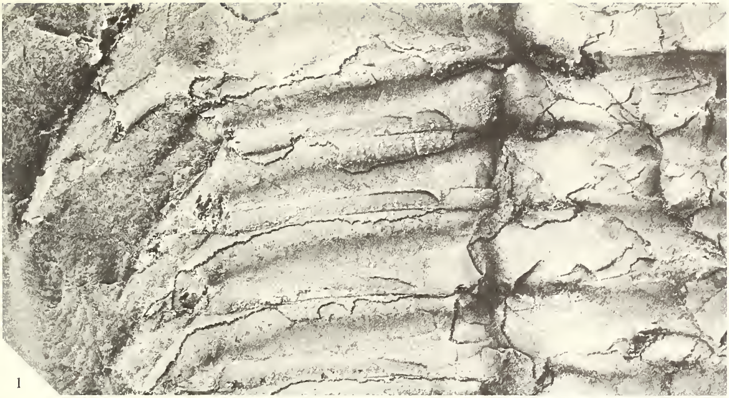
EXPLANATION OF PLATE 17

Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

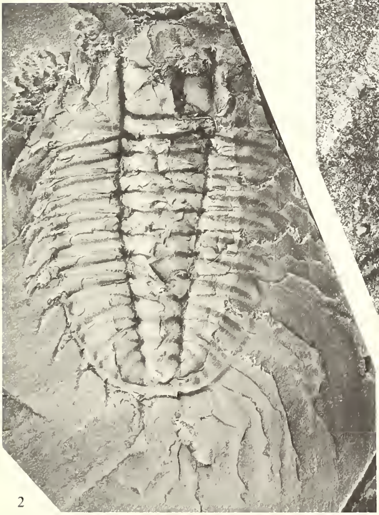
Fig. 1. G.S.C. 34694, level 6 ft 7·5 in. to 7 ft 3·5 in. Portions of posterior border of cephalon and thoracic segments 1–4, × 5. For interpretation see text-fig. 1.

Fig. 2. G.S.C. 34694, level as fig. 1, entire, × 1·25.

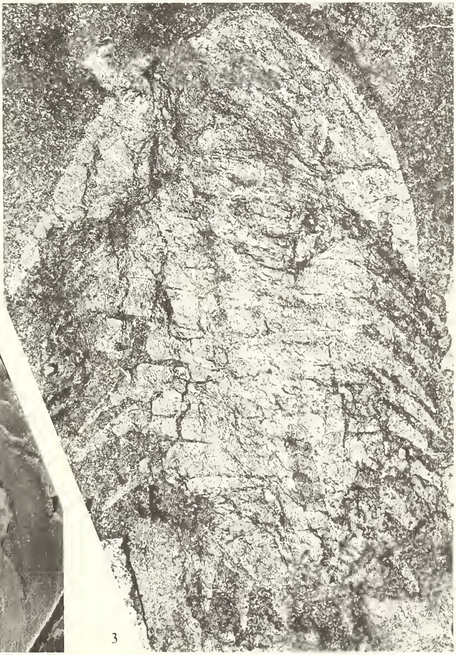
Fig. 3. U.S.N.M. 194000, under water, × 5.



1

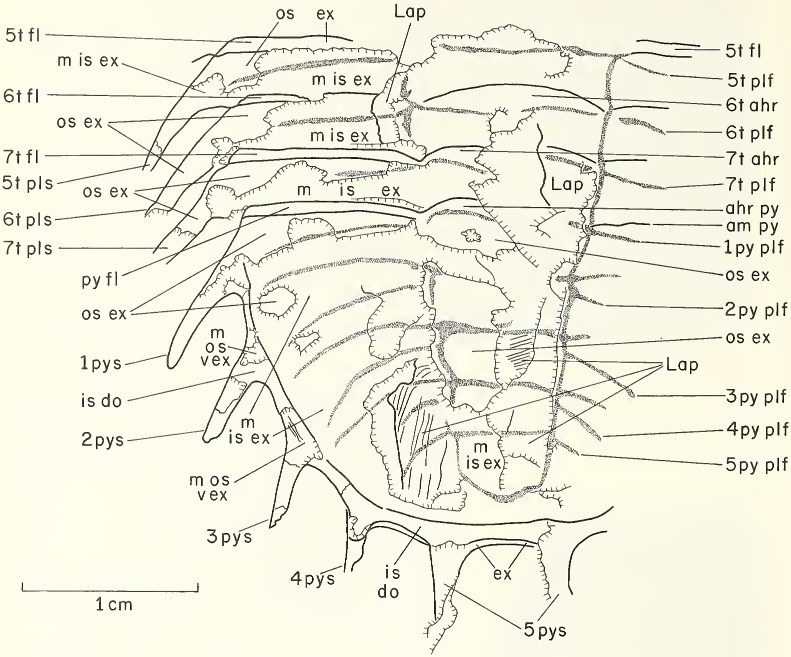


2



3

WHITTINGTON, *Olenoides*



TEXT-FIG. 2. Explanatory drawing of axial region and left pleural region of last three thoracic segments and pygidium of original of Plate 18, fig. 2.

EXPLANATION OF PLATE 18

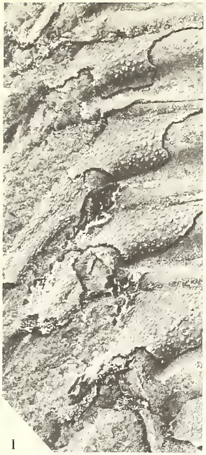
Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

Fig. 1. G.S.C. 34694, level 6 ft 7·5 in. to 7 ft 3·5 in. Distal portions of left thoracic pleurae 4–7 and the first pygidial pleura, showing details of external surface, × 5·5.

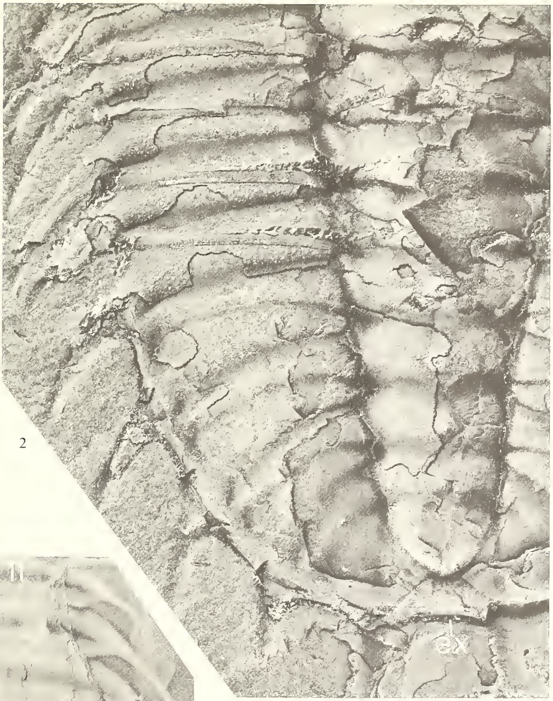
Fig. 2. G.S.C. 34694, level as fig. 1. Portions of thoracic segments 4–7 and pygidium, × 4. For interpretation see text-fig. 2.

Fig. 3. G.S.C. 61374, level 5 ft 5 in. to 6 ft 2 in. Right side of axial region of thoracic segments 1–7 and a portion of the pygidium, × 3. Portions of right pleurae covered by a thin layer of shale, through which form of pleurae and pleural spines has been impressed by compaction.

Fig. 4. G.S.C. 34694, level as fig. 1, left half of glabella and portion of cheek lobe, × 4. Fragments of exoskeletal layer showing external surface, adhere to anterior portion of glabella, palpebral lobe, and adjacent areas of cheek and border.



1



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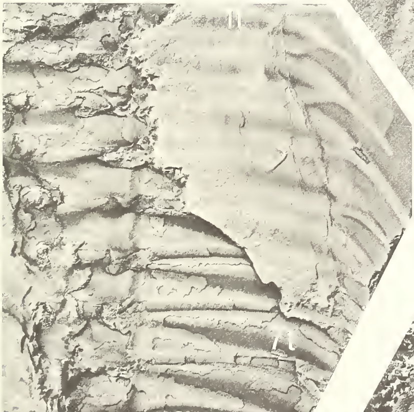

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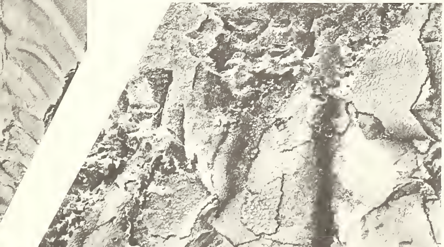


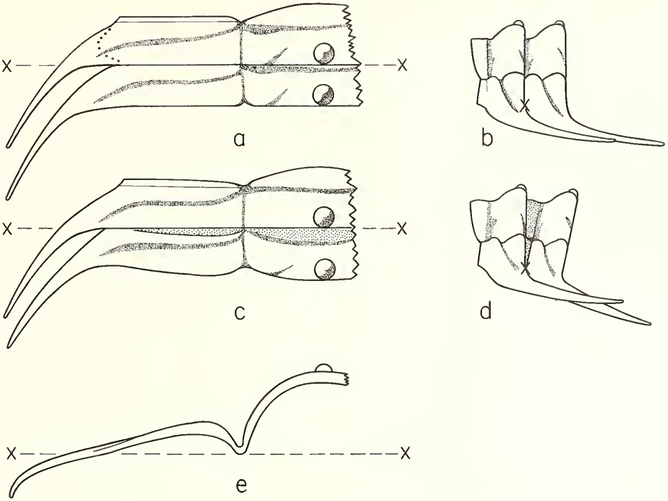
4

WHITTINGTON, *Olenoides*

margin of the doublure curves around to meet the posterior margin of the pleura a short distance inside the base of the pleural spine. The flange thus appears to have lain beneath the dorsal exoskeleton of the preceding pleura; only distally may it have passed beneath a narrow strip of doublure. The articulating half-ring is of length (sag.) about one-third that of the axial ring. A median posterior tubercle is present on each axial ring and the first four of the pygidium. Most specimens split to reveal the inner surface of the exoskeleton of the thoracic rings, the outer is rarely preserved. One exception (Pl. 18, fig. 3) has the median tubercle of the last thoracic segment prolonged into a short backwardly directed spine, possibly other thoracic median tubercles were similar; those of the pygidium are steep on the posterior side.

In preparing restorations of *Olenoides serratus* (Whittington 1975, p. 122) I made certain assumptions about original convexity of the exoskeleton. That of the pygidium was based on the pygidium of a different species illustrated by Fritz (1968, pl. 39, figs. 4, 5). I assumed that the inner portion of the thoracic pleura was horizontal, because the hinge between it and the next pleura must have run along it, and that the outer portion, the pleural spine, was probably directed gently downwards. It is difficult to assess from 34694 or other specimens the extent of the flattening that has taken place. Cracks and vertical displacement of parts are characteristic of the cephalon, and the hypostome is commonly pressed against the underside of the glabella (Pl. 17, fig. 2; Whittington 1975, pl. 1, figs. 2, 3). Axial rings of the thorax characteristically show a longitudinal zigzag crack, suggestive of the strong original convexity. The axial region of the pygidium is not so cracked, nor are the pleural regions of thorax and pygidium. There are longitudinal cracks in pleural spines, but not transverse fractures as might be expected if the spines had been steeply inclined. In the present restoration (text-fig. 3) the axial ring is accordingly strongly convex, the pleura (including the flange) is gently convex transversely, and the pleural spine is gently downwardly inclined. There is no evidence of geniculation at a fulcrum in the pleura, so I abandon my earlier view that the inner portion was horizontal, the outer flexed down. The position of the hinge line means that on flexure both articulating half-ring and flange would have moved back relative to the segment in front, covering the gap as it opened (text-fig. 3*c*, *d*). The axial furrow is shallow and broad between axial ring and posterior pleural band, but deepens as it descends to either margin. The narrow (exs.) band that connects flange and articulating half-ring shows no evidence of an axial process, so that I do not accept the view of Bergström (1973, p. 22) that such an articulating process is present. The antero-lateral angle of the flange is rounded, and affords no evidence of a fulcral process. Instead of such a process, the distal portion of the flange helped to maintain each pleura in the correct position relative to those adjacent. I consider it unlikely that the pleura sloped more steeply outwards than shown in text-fig. 3*e*, because this would have meant that the hinge line would have run below the level of the axial furrow, and that therefore on flexure a gap would have opened at this furrow as well as along the entire axial ring and adjacent portion of the pleura. Such a gap, on flexure of the amount shown in text-fig. 3*c*, *d*, would not have been bridged by the articulating half-ring and flange.

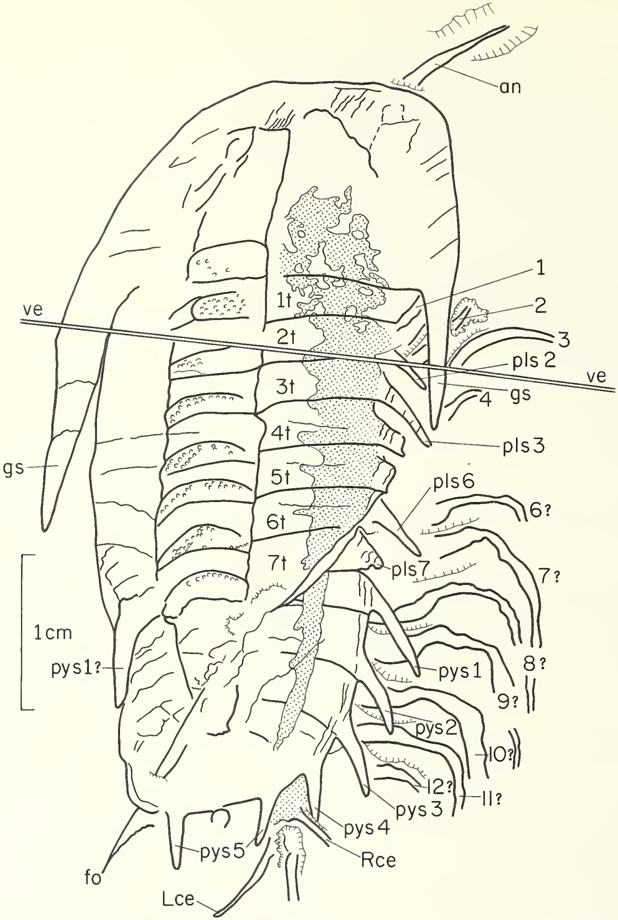
The morphology and manner of articulation of the thorax of *O. serratus* is in sharp contrast to that occurring in the Lower Cambrian *Crassifimbria walcotti* (Palmer 1958, pp. 159–160, text-fig. 5) and the Middle Cambrian *Bolaspidella housensis* (Robison 1964, pl. 89, figs. 8, 9). In these species the inner portion of the pleura is horizontal, the outer part flexed down at the fulcrum, the hinge line lying along the straight edge of the inner portion; the outer portion is facetted, and Palmer describes the device which limits enrolment. This type of articulation is characteristic in post-Cambrian trilobites (Whittington and Evitt 1954, pp. 21–24), and may be aided by ball-and-socket joints. In *O. serratus* there is no clearly defined fulcrum, ball-and-socket joints do not appear to be developed, but the flange acts distally as a guide and medially as a protection during flexure. This situation is similar to that in redlichiids and olenellids (Öpik 1970, pp. 3–5; Bergström 1973, p. 17, pl. 2, fig. 4), in which the fulcrum was absent and the pleura curved down distally, each guided under the one in front during enrolment by an antero-lateral projection. The development of the broad flange in *O. serratus* is distinctive, indicative of the variety of modes of articulation in Cambrian trilobites.



TEXT-FIG. 3. Restoration of left halves of two mid-thoracic segments of *Olenoides serratus*, in extended (*a*, *b*) and flexed (*c*, *d*) positions, respectively dorsal and left lateral views. *e*, posterior view. × and dashed line indicate position of hinge line, coarse stipple on portions of flange and articulating half-ring exposed by flexure. Dotted line on left side of anterior segment in (*a*) indicates position of inner margin of doublure.

THE NEWLY MOULTED EXOSKELETON, '*NATHORSTIA TRANSITANS* WALCOTT, 1912'

Henningsmoen (1975) remarked that if a newly moulted individual were preserved, it might well be wrinkled and deformed, and mistaken for a new species. This was the case with '*Nathorstia transitans*', a deformed specimen described as a new genus and species by Walcott (1912, pp. 191, 194-195, 216, pl. 28, fig. 2). In low-angle radiation (Pl. 19, figs. 3, 4) the specimen appears only slightly darker than the surrounding rock, and in contrast to specimens of *O. serratus* (Pl. 17, fig. 2) it shows little relief and the surface has a wrinkled appearance. There is no mineralized exoskeletal layer, the glabella in front of the occipital ring is defined only on the right side, and eye lobe, eye ridge, and facial suture cannot be seen, wrinkling being conspicuous on the cephalon. The rings of the axial region of thorax and pygidium are visible, the posterior portion of each thoracic ring showing a transverse granulated band. Interpleural furrows are best defined as narrow ridges on the counterpart (Pl. 19, fig. 4), pleural furrows can scarcely be detected. Preparation has revealed the genal spines, and in the counterpart (left side of Pl. 19, figs. 2, 4) right pleural spines 3 and 6, and right pygidial border spines 1-5. Portions of appendages appear as darker strips on the right side, outside and postero-lateral to the exoskeleton. Walcott's illustration was of the part only, photographed in a manner which reflected light from the specimen. In reflected radiation (Pl. 19, figs. 1, 2), part and counterpart show particularly clearly the appendages and genal and border spines. The part shows as a reflective area the trace of the alimentary canal, broadest anteriorly,



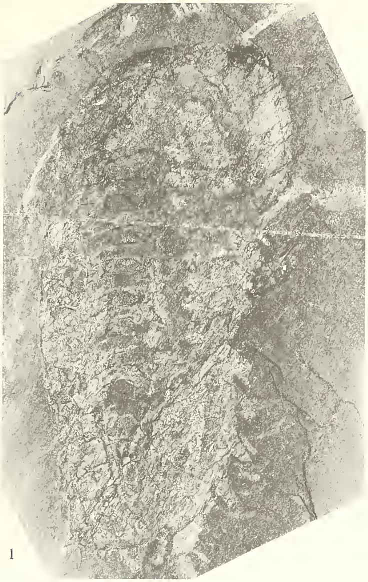
TEXT-FIG. 4. Composite explanatory drawing of U.S.N.M. 57685, cf. Plate 19, figs. 1–4. Stippled area is trace of alimentary canal.

EXPLANATION OF PLATE 19

Olenoides serratus (Rominger, 1887). U.S.N.M. 57685, holotype of *Nathorstia transitans* Walcott, 1912, Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia. For interpretation see text-fig. 4.

Figs. 1, 3. Original of Walcott, 1912, pl. 28, fig. 2, respectively under water, ×2; west, ×1·5.

Figs. 2, 4. Counterpart, respectively under water, ×2; showing posterior portion of cephalon, thorax, pygidium, and portions of appendages, north-west, ×2.



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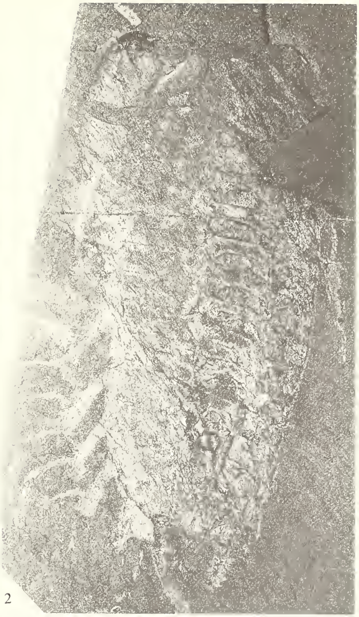

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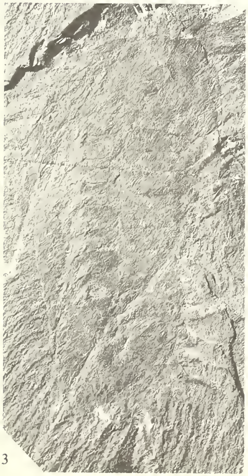

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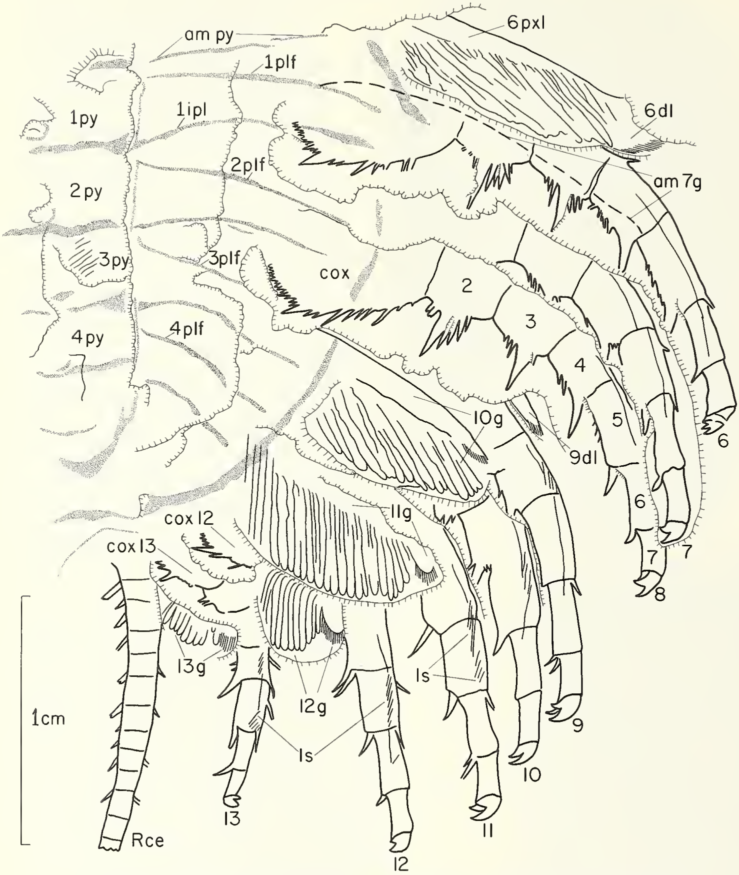
WHITTINGTON, *Olenoides*



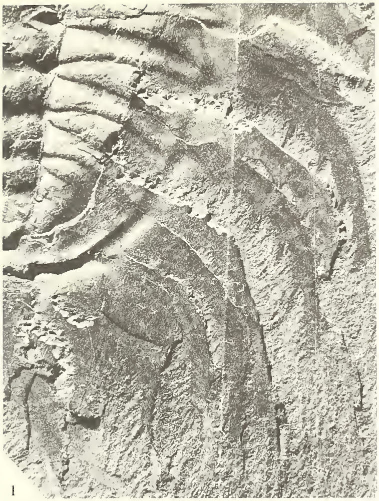
TEXT-FIG. 5. Composite explanatory drawing of G.S.C. 34694, cf. Plate 20, figs. 1–4.

EXPLANATION OF PLATE 20

Olenoides serratus (Rominger, 1887). G.S.C. 34694, Phyllopod bed, level 6 ft 7·5 in. to 7 ft 3·5 in., Middle Cambrian, Burgess Shale, British Columbia. For interpretation see text-fig. 5.

Figs. 1, 2. Right half of pygidium and appendages, respectively north-west, under water, ×2·5.

Figs. 3, 4. Counterpart, right half of pygidium and appendages, respectively south, under water, ×2·5.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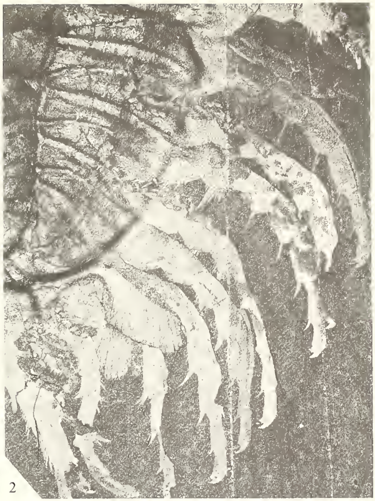
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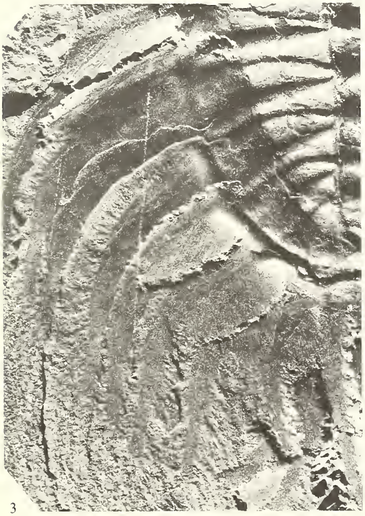
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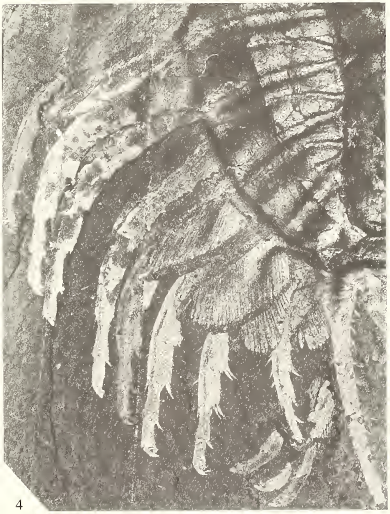
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WHITTINGTON, *Olenoides*

medially and posteriorly having lobate projections which may be traces of proximal portions of diverticulae (text-fig. 4). In ordinary light portions of this area are stained yellow-brown.

My interpretation (text-fig. 4) differs from that of Walcott's (1912, pl. 28, fig. 2) retouched figure. He shows the right eye lobe as a strongly reflective crescent, but no such feature can be traced on part or counterpart (Pl. 19, figs. 1, 2). The antenna, poorly preserved leg branches, and cerci were shown by Walcott, but he labelled the left genal spine as a 'leg (mandible?)', and the proximal portions of pygidial border spines 2 and 3 as 'thoracic legs'. He considered that the proximal podomeres of the limbs were setose, but I cannot confirm this observation. He also mentions 'indications of a branchial lobe' in two other specimens, but no such specimens are preserved and labelled in his collections. He writes of the leg branches having been 'pushed out from beneath the dorsal shield'. It appears that the traces of both alimentary canal and appendages have been moved the same distance to the right relative to the exoskeleton. Such displacement is invariable in specimens of *O. serratus* (Whittington 1975, pp. 103–104, fig. 2).

Raymond (1920, p. 31) suggested that this specimen was a recently moulted *O. serratus* because of its appearance as a shadowy impression, and because the outline, position of eye lobe, pygidial spines, and presence of cerci, are all like that species. This opinion has been repeated (Størmer 1942, p. 147; Hupé *in* Piveteau 1953, p. 149; Harrington *in* Moore 1959, p. O76, O149), and is reinforced by this investigation. The size of the specimen, relative size of cephalon and pygidium, the thorax of seven segments, the shape, length, and direction of genal, pleural, and pygidial border spines, all agree to suggest that it should be assigned to *O. serratus* and not to any other species (see lists in Rasetti 1951, pp. 103–104; Fritz 1971, fig. 5) occurring at the same horizon. Simonetta and Delle Cave (1975, p. 6) questioned this identification because of the apparent absence of pleural spines, but this view is no longer tenable. It is typical of the way in which *O. serratus* is preserved in showing displacement of soft parts relative to the exoskeleton. Not only does the latter appear to be unmineralized, but the outline is asymmetrical, and pleural and pygidial spines are present on the right but not on the left side. These features are consistent with the carcass having been buried at an oblique angle to the bedding, tilted down to the left, and inclined forwards and downwards, and subsequently compressed (compare discussion of preservation of *Naraoia* in Whittington 1977, pp. 413–416, figs. 1, 3). To this attitude of burial may be related the direction of the wrinkling and fold in the specimen, the displacement of soft parts, and other features. The absence of traces of sutures is consistent with the supposed newly moulted condition of the animal.

The 1975 study was based on thirty examples of *O. serratus* (fifteen from the Walcott collection, U.S. National Museum) which had the appendages preserved and the exoskeleton mineralized; the range in exoskeletal length (sag.) lies between 5·2 and 8·1 cm (Whittington 1975, pp. 101–102, 128). The smallest specimen is thus only slightly longer than 57685 (length (sag.) 4·8 cm). An intensive search of the Walcott collection has revealed only one other (Pl. 17, fig. 3) example which lacks the mineralized exoskeletal layer with a length (sag.) of 2·2 cm. The exoskeleton is slightly distorted, preserved as a wrinkled, reflective film, showing no trace of appendages. It is exposed from the ventral side, and shows the narrow doublure of cephalon and pygidium, traversed by thin lines subparallel to the margins. Outline, relative size of cephalon and pygidium, seven thoracic segments, size, direction, and form of genal, pleural, and pygidial border spines are typical of

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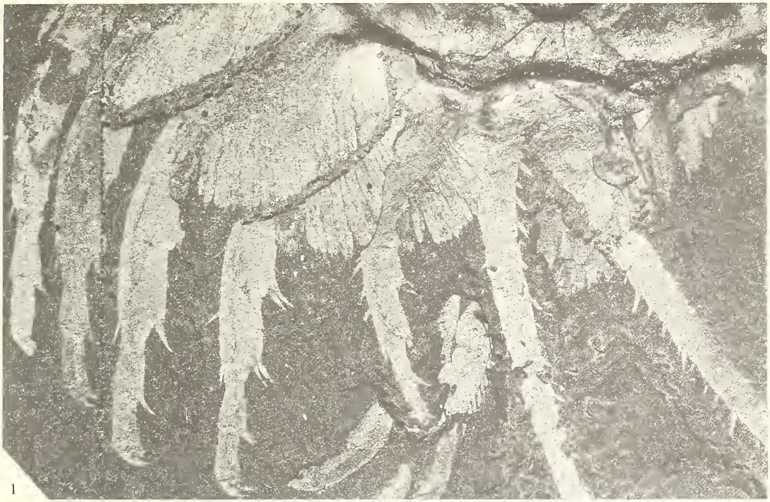
EXPLANATION OF PLATE 21

Olenoides serratus (Rominger, 1887). G.S.C. 34694, Phyllopod bed, level 6 ft 7·5 in. to 7 ft 3·5 in., Middle Cambrian, Burgess Shale, British Columbia. See text-fig. 5.

Fig. 1. Counterpart, details of right appendages 9–13 and cerci, under water, × 5.

Fig. 2. Details of ventral and inner margins of coxae 6 and 8, ventral spines of podomere 2 of leg branch 8, under water, × 10.

Fig. 3. Details of ventral margin of coxa 12, lamellae of gill branch 12, coxa and podomeres 2–5 of limb 13, under water, × 5. To lower left is portion of left limb 11.



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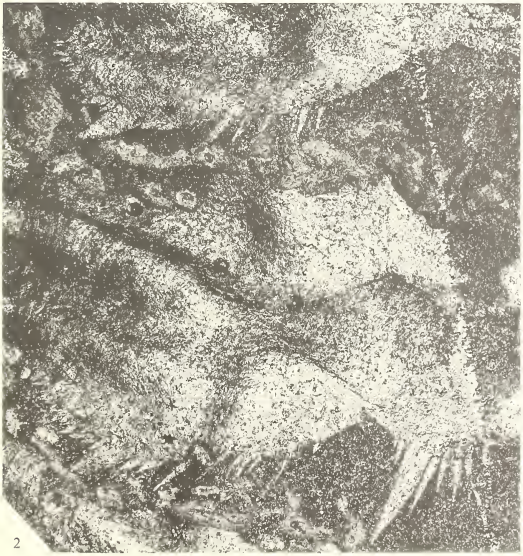

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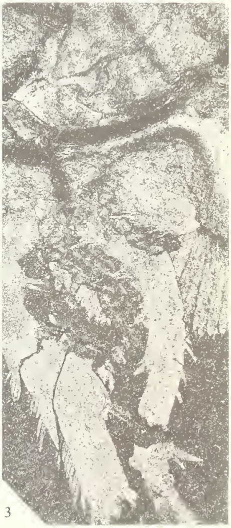

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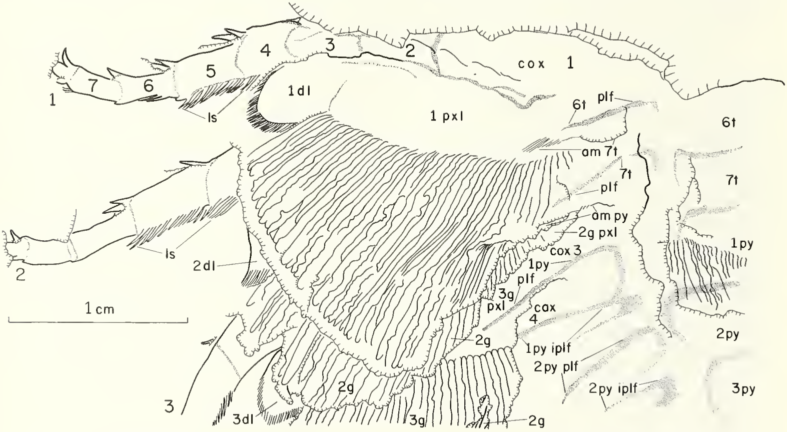
WHITTINGTON, *Olenoides*

O. serratus. It differs from Walcott's type in that the broad, parallel-sided glabella, extending forwards to the border furrow, is outlined. On the right cheek close to the mid-part of the glabella is a curved, reflective strip probably representing the eye lobe, and the course of the facial suture may be traced.

FUNCTIONAL MORPHOLOGY OF THE BIRAMOUS APPENDAGE

Morphology and attitude on burial. Two specimens have been prepared further and selected for re-illustration, not only because they show the morphology of the appendage in detail, but because they show two characteristic ways in which the branches are preserved. In text-fig. 5 (cf. Pl. 20, figs. 1–4) the successive coxae and leg branches are curved through 60° to 80°, and inclined backwards and downwards at a slight angle to the bedding plane, so that each passes below the one following. The inner margin shows rows and groups of spines, the outer a smoother curve showing rare small spines. Inside this outer margin in podomeres 4, 5, and the proximal portion of 6, is a narrow band along which oblique striations are rarely visible (Pl. 21, fig. 1). This band appears to be the trace of the lateral spines flattened against the surface. The outer branch lies on, and in leg branches 6–10 partly in front of, the leg branch, the lobate portion is narrow (exs.), the lamellae short and strongly outwardly directed. This appearance is in sharp contrast to that of the outer branch of appendage 1 in text-fig. 6 (cf. Pl. 22, figs. 1, 2), which lies behind the leg branch;



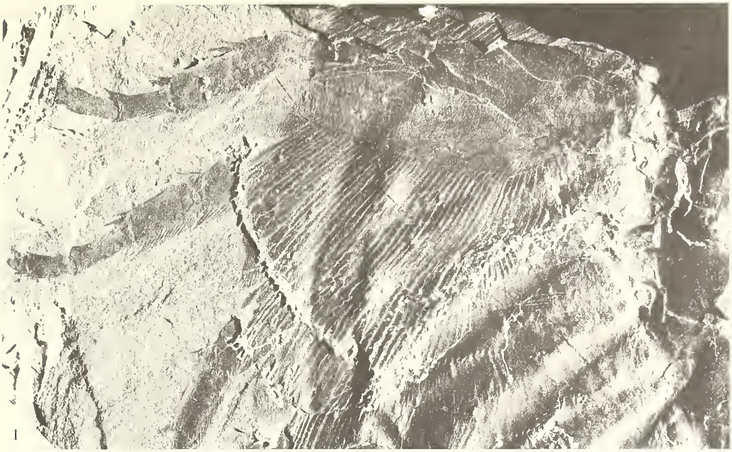
TEXT-FIG. 6. Explanatory drawing of portion of the counterpart of G.S.C. 34695, cf. Plate 22, figs. 1, 2.

EXPLANATION OF PLATE 22

Olenoides serratus (Rominger, 1887). Phyllopod bed, Middle Cambrian, Burgess Shale, British Columbia.

Figs. 1, 2. G.S.C. 34695, level 6 ft 11 in. to 7 ft 0 in., counterpart, respectively west, under water, × 3·3. For interpretation see text-fig. 6.

Fig. 3. G.S.C. 34697, level 6 ft 11 in. to 7 ft 2 in., gill branch and portion of leg branch of left side, showing fine hairs at tips of distal lamellae of gill branch, reflected, × 5.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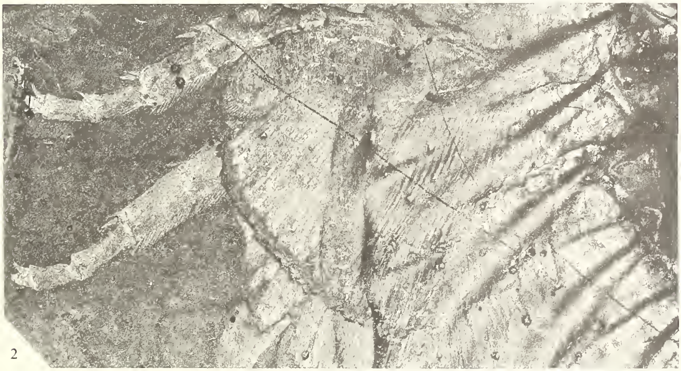
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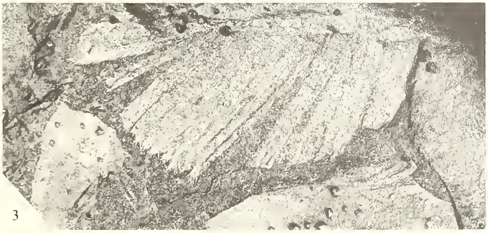
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WHITTINGTON, *Olenoides*

the proximal and distal lobes are wide, the lamellae long and arranged fan-wise. The leg branch is extended in an 'S' curve, rows of fine spines extend from the margins of podomeres 4 and 5, and the distal claws are spread in a group of three, the median largest, not curved inwards in an overlapping group. In text-figs. 7, 8, I reconstruct the morphology of the appendage in a way that is consistent with explaining these different appearances as resulting from different attitudes on burial and the effect of compaction. In text-fig. 7, two appendages are shown in the burial position of 34694, the posterior side of the antero-posteriorly flattened coxa and leg branch towards the observer, the outer branch directed up towards the observer, and hence foreshortened. Compression vertical to the bedding plane would give the appearance seen in 34694, the outwardly directed spines on podomeres 4 and 5 of the leg branch being flattened against the wall of the podomere. Text-fig. 8 shows two appendages, viewed obliquely, in the burial position of 34695. Compression vertical to the plane of bedding would result in the outer branch lying undistorted, but coxa and leg branch being compressed obliquely (postero-ventrally). Thus the ventral spines of podomeres 4 to 6 came to lie on one side of the leg, the row of lateral spines on podomeres 4 and 5 form a row on the opposite side, and the terminal claws are divergent. Text-figs. 7, 8 show the spines of the coxa, and ventral spines of podomeres 2–6, in more detail than the 1975 reconstructions. The lateral spines of podomeres 4–6 are termed spines rather than setae because of the tapering, thorn-like form. They arise from the probably curved antero-dorsal and postero-dorsal surfaces of the podomeres; the rare spines on the dorsal side of the leg (Pl. 21, fig. 1) may be lateral spines displaced during burial.

Other examples of the two kinds of preservation discussed above are shown by the specimens previously described. In numbers 58588A, 58588B, 58589 (left limbs 5–7), and 65514 (right appendages 3–6), illustrated in Whittington 1975, pls. 2, 4, 5, 10, the appearance is like that of appendages 6–8 of 34694. The attitude seen in appendages 1–3 of 34695 is displayed by appendages of 65513, left 8–15 of 65514, and those of the right side of 34697 (Whittington 1975, pls. 7, 10, 24). As might be expected, not all specimens fit into these categories, or even intermediates between them, because of the varied attitudes on burial. The two examples selected here show the following features of preservation that are common to all specimens of *O. serratus* which have a mineralized exoskeleton and show traces of appendages (Whittington 1975, pp. 102–104, 127):

(i) The appendages are in an original serial relationship to each other, but displaced relative to the exoskeleton. In each example the coxae lie beneath the pleural region, beneath the outermost portion in 34694.

(ii) Successive branches in a series are imbricated, the lamellae of the outer branch extending backwards dorsal to the one following, each leg passing below (ventral to) the one following. A thin layer of rock separates successive branches, and the branches from the exoskeleton. These rock layers are shown by the minute scarps that intervene between successive branches. The scarps were produced when the rock was split, or by preparation, and are shown by hachures in the text-figures.

(iii) Leg branch and outer branch extend out in the same direction from the coxa, are not divergent, and are not disposed at varying angles to each other.

(iv) The body has been compressed, so that while the exoskeleton shows relief (reduced from the original) the appendages are preserved as an extremely thin layer, darker than the shale, and reflective; the reflectivity varies from specimen to specimen. Furrows and ridges in the exoskeleton have been impressed on to the appendages.

Function of outer branch. The four features of preservation discussed above imply that:

(*a*) the long lamellae of the outer branch were extended backwards and slightly upwards in life, over the next one or two succeeding appendages (Whittington 1975, fig. 27). The outer branch and leg branch are never preserved in an alternating, imbricated series, as they might have been if the outer branch had been rotated so that the lamellae were downwardly directed. The length of the lamellae, and their apparent stiffness (apparent because in any one branch they are preserved subparallel, rarely displaced), appears to have precluded their being swung down between successive limbs.

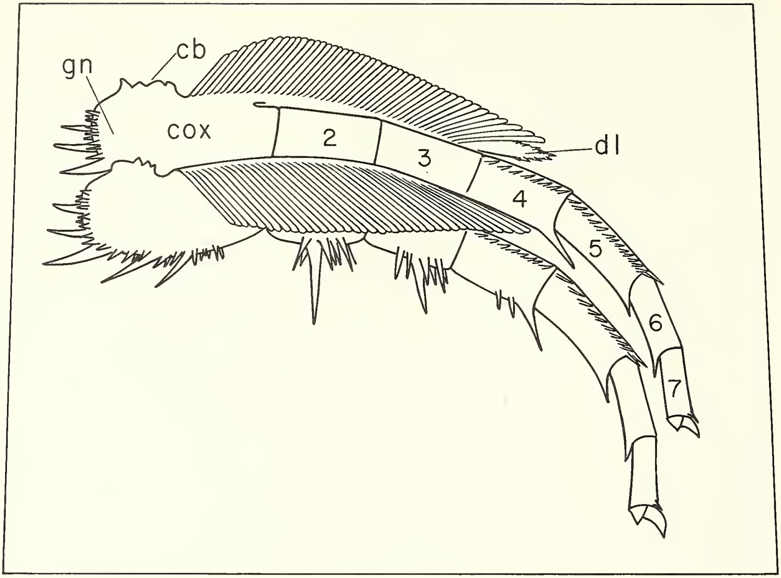
(*b*) proximally the outer branch was attached to the inner, postero-dorsal edge of the coxa, adjacent to the coxa-body junction (text-fig. 6). The distinctive way in which each series of branches is preserved, and the attitude in which the two branches appear to have been buried (text-figs. 7, 8), implies that this attachment was relatively rigid. There is no evidence that the outer branch could rotate or swing to and fro about the junction with the coxa.

These implications mean that the outer branches of the appendages in *O. serratus* were imbricated close beneath the ventral cuticle of the pleural regions, and cannot have been used to rake the sediment surface. Their position does not encourage the view that food particles were trapped by the lamellae. There seems no arrangement by which such particles could have been scraped off, collected, and conveyed to the mouth. The lamellae are preserved as long, flat strips, imbricated, the edge nearer the observer ragged as a result of breakage (Pl. 22, figs. 1, 2). The tip of each lamella is rounded and bears a few, fine setae (Pl. 22, fig. 3). The lamellae may have had the form of long, thin slats (Whittington 1975, p. 127).

A rough calculation, based on my restoration (1975, fig. 25) suggests that the combined areas of the outer surfaces of the filaments of the limb series was three times that of the ventral integument of the pleural regions. This integument is known only from the dark area in the centre of the appendages in 34692 (Whittington 1975, fig. 20; pl. 17, fig. 1), which reveals nothing of its structure. Oxygen could have been absorbed through it; whether or not it bore special gill structures (Bergström 1969, pp. 410–411) is unknown. I conclude that the primary function of the outer branches of the appendages in *O. serratus* was in respiration, and that the animal was not a filter feeder.

A more difficult question is on the possible function of the gill branch in swimming (Whittington 1975, p. 132, fig. 30). Once launched off the bottom (see next section) the coxae and leg branches would have to have been swung back into a trailing position to lessen their resistance to forward progress. If the junction between outer branch and coxae was relatively rigid, as implied above, the outer branch would have been pressed against the ventral cuticle, to an amount dependent upon the flexibility of the long lamellae. Only intrinsic musculature within the lobate portion of the outer branch could have enabled the outer branch to have been moved away from the ventral cuticle and back, to suck in and expel water and create a current that might have aided swimming. Whether such musculature was present is unknown, and the swimming powers of *O. serratus*, which may have been caused by such movements in a metachronal rhythm, are uncertain. Perhaps *O. serratus* had little or no swimming ability.

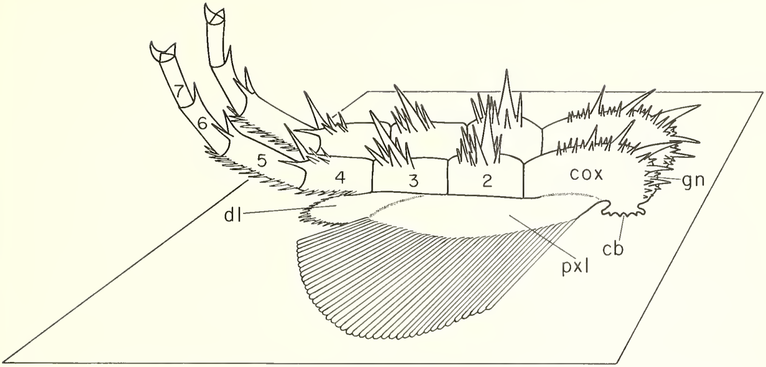
Outer branch of other species. The nature of this branch is not as well known in other species. For example, the basis for the reconstruction by Cisne (1975, figs. 1–3, pp. 47, 53–54) of the exite of *Triarthrus eatoni* has not been fully documented, but he shows the series as imbricated in the same sense as in *O. serratus*, and remarks that it was 'rather stiff and rigidly attached to the coxa'. Bergström's views on the nature and function of the exite were partly based on his reconstruction of the exite of *Cryptolithus* (1972, pp. 87–89, fig. 2). This reconstruction was modified without comment by Bergström (1973, fig. 15), and a quite different reconstruction is given by Campbell (1975, pp. 68–69, fig. 13). Dr. Campbell informs me (pers. comm.) that his figure 13 is a ventral view, and it is much more like the original of Raymond (1920, fig. 20) than are Bergström's reconstructions. Campbell used his reconstruction in the interpretation of burrows attributed to *Cryptolithus*, remarking that certain striations 'must have been produced by the ends of the exites that moved so as to shift sediment backwards and inwards towards the midline' (Campbell 1975, p. 70). Subsequently Campbell (1975, p. 81) explains that it is the ends of the lateral filaments of the branch that he considered were used to assist in digging, while more proximal filaments were used in respiration and to trap food particles. These ideas require that the exite shaft could be rotated about its axis to bring the filaments into a vertical position between the walking legs (Campbell 1975, fig. 14), and that the shaft could be flexed back and forth to sweep sediment



TEXT-FIG. 7. Diagram to explain the attitude in which appendages were buried on the right side of G.S.C. 34694. Two successive right appendages are shown, the posterior surface of coxa and leg branch towards observer and imbricated subparallel to the bedding, the gill branch projecting up towards the observer. View slightly postero-oblique to vertical, bedding plane shown tilted down away from observer, at acute angle to surface of page. Filaments of gill branches projecting upwards at slightly different angles. Compression vertical to the bedding plane, accompanying compaction, would result in the appearance shown by appendages 6 and 9 respectively of 34694 (text-fig. 5; Pl. 20, figs. 1-4). The gill branch appears short (exs.) compared to 34695, the lamellae directed strongly outwards, and, depending on the exact attitude prior to burial, the gill branch may lie partly in front of (appendages 6-9 of 34694), or on and behind the leg branch (appendages 11-13).

particles. Yet if Campbell's reconstruction (1975, fig. 13) is accepted, and the filaments were stiff enough to be used in excavation of a burrow, the overlap of one exite over that following, is too great to allow the filaments to be swung down past each other to a vertical position. A critical reinvestigation of the appendages of *Cryptolithus* is needed before there can be further discussion of function, for Campbell's suggestions seem open to question, particularly the assumption that exite filaments were used in excavation of a burrow. The recent reinvestigation of the Devonian *Phacops* (Stürmer and Bergström 1973) shows little of the outer appendage branch. It appears that, in genera other than *Olenoides*, the morphology and attitude of the outer branch is so poorly known that speculation on function is hazardous.

Function of coxa and inner branch. The inner, dorsal portion of the coxa is not preserved in any specimen, and traces of the ventral cuticle were found in only one example. The implication is that this cuticle was thin and little sclerotized, in contrast to that of the major portion of the coxa and

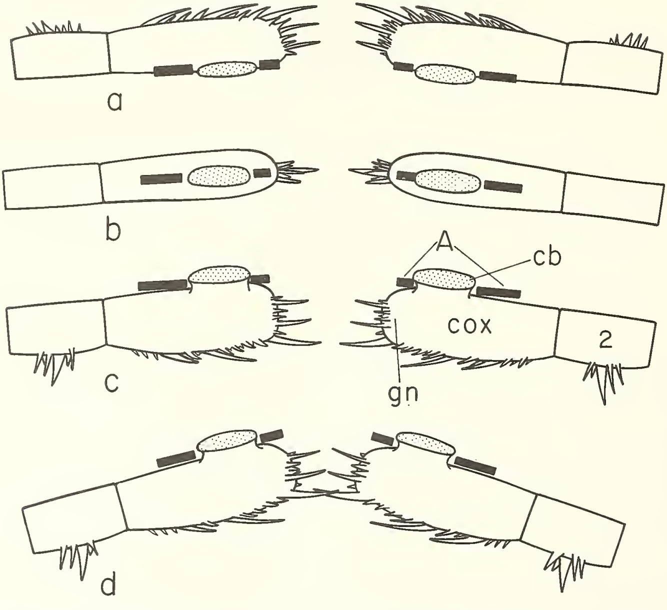


TEXT-FIG. 8. Diagram to explain the attitude in which appendages were buried in G.S.C. 34695. Two successive right appendages are shown, the gill branch lying (ventral surface visible to observer) parallel to the bedding, the posterior surface of the coxa and curved leg branch towards observer, inclined upwards and slightly forwards relative to the bedding plane. Oblique view, bedding plane outlined. The gill branch of the farther appendage is completely concealed beneath that of the nearer limb. Compression vertical to the bedding plane, accompanying compaction, would result in the appearance shown by appendages 1 and 2 of 34695 (text-fig. 6; Pl. 22, figs. 1, 2). In this specimen, preparation of gill branch 1 has revealed the complete medial and distal filaments which would have been concealed beneath portions of appendages 2 and 3.

the leg branch. The coxa appears to have been joined to the ventral cuticle adaxially (text-figs. 7, 8; cf. Whittington 1975, p. 129). Because of the thinness of the cuticle at the junction, an appropriate arrangement of extrinsic coxal muscles may have allowed considerable freedom of movement, but these movements would have been weak (cf. Manton 1977, p. 52). The specimens afford no evidence of a heavily sclerotized ventral cuticle, to which the coxa was articulated at a joint.

At the junctions between podomeres of the inner branch (Whittington 1975, p. 123, fig. 29), the dorsal margin is not sharply stepped, though interrupted at the podomere 5–6 junction by a small spine (legs 6 and 7, text-fig. 5; Pl. 20, figs. 2, 4; Pl. 21, fig. 1). The ventral margins between coxa and podomere 2, and podomeres 2 and 3, are also at the same level. These joints may have been pivot joints (Manton 1977, fig. 2.2d; text-fig. 10), that is, may have allowed movement up and down. The S-shaped curvature of the limb seen in 34695 (text-fig. 6) and other examples, implies a slight upward bend of the proximal portion of the branch, such as hinge joints would have made possible. The ventral margin at the articulations between podomeres 3–4, 4–5, 5–6, and 6–7 shows a step, with spines projecting from the step between each of the latter three articulations. There was probably a hinge joint (Manton 1977, fig. 2.2e; text-fig. 10) at the dorsal edge. Thus the coxa and leg branch could have been flexed into a curve subtending 180° or more, or extended straight or slightly upwards, only in the axial plane of the antero-posteriorly flattened limb. Overlapping rows of large and small spines are seen on the ventral and inner (gnathobasic) margins of coxae 6, 8, 12, and 13 of 34694 (Pl. 21, figs. 2, 3), and main and smaller spines on the ventral side of podomeres 2 and 3, and smaller spines at the junctions of more distal podomeres (Pl. 20, figs. 2, 4). This armature extended from the anterior (Whittington 1975, pl. 7, figs. 1–4; fig. 10) to the posterior (Pl. 21, fig. 3) appendages of the complete series, so that *O. serratus* could have used the entire series of limbs to seize and hold prey or decayed material. A median groove, flanked by the gnathobases, extended from the mid-length of the pygidium forwards to the mouth. The manner by which soft food was squeezed, shredded, and passed forwards to the mouth by the pairs of gnathobases was described previously (Whittington 1975, p. 133). Text-fig. 9 is an attempt to show this action of a pair of gnathobases, and probable similar movements in *Triarthrus* have been advocated by Manton (1977, pp. 52–53).

The specimens do not show the original position on the body of the relatively small coxa–body junction, but it seems reasonable to assume that it was approximately as shown in text-fig. 10 (cf. Whittington 1975, figs. 25, 26), i.e. each pair of gnathobases was relatively closely opposed (text-fig. 9). The principal movement of the coxa and leg branch was a promotor–remotor swing about an approximately transverse axis through the coxa–body junction. This swing of the series



TEXT-FIG. 9. Diagrams in dorsal view of the coxa and podomere 2 of a pair of leg branches, showing the results of movements at the coxa–body junction. An axis of swing (A) at the junction is shown as a solid black bar, the axis in *a*, *b*, *c*, directed outwards and slightly backwards at 5° to the transverse plane. *a*, at limit of promotor swing, coxa and podomere 2 in oblique anterodorsal aspect, maximum separation between gnathobases. *b*, coxa and podomere 2 vertical, in dorsal aspect. *c*, at limit of remotor swing, coxa and podomere 2 in oblique postero-dorsal aspect, gnathobases at closest approach. Coxa–body junction stippled. The limb at the limit of the remotor swing (*c*) is at a greater angle to the transverse, vertical plane than the limb at the limit of the promotor swing (*a*). *d*, as (*c*), but with a slight adduction of the coxae and a twist at the coxa–body junction (clockwise on the right, anticlockwise on the left) so that the axis of swing is inclined at about 15° to the transverse plane. The effect is to bring the gnathobases closer together and slightly forward of the position in (*c*).

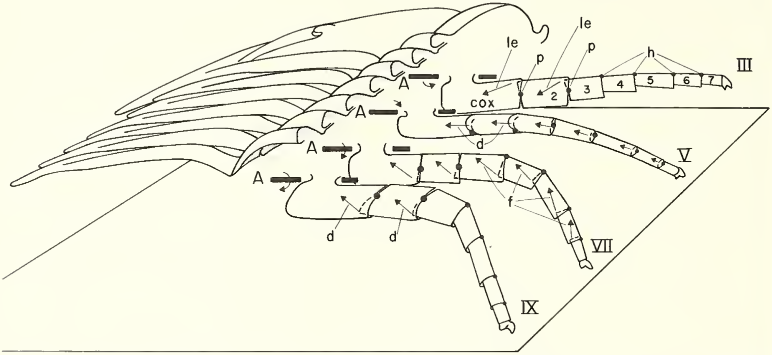
of limbs in a metachronal rhythm in walking, is discussed in the succeeding section. In text-fig. 9*a–c*, it is suggested that the axis of swing was directed outwards and slightly backwards, and the effect is that the gnathobases are closest at the end of the remotor swing, and move further apart during the promotor swing. Thus food could be squeezed and released to the next pair of coxae in front, and so passed forwards to the mouth. This effect could have been aided by slight adduction of the coxae combined with a slight twist of the axis at the end of the backstroke (text-fig. 9*d*). Such movements could have been made possible by appropriate extrinsic musculature, because the coxa was joined to the flexible ventral cuticle of the body. This junction having been relatively small and not rigid, these movements would have been adequate for squeezing and shredding soft food and passing it forwards, but would not have provided a strong biting and crushing mechanism.

The distal podomere (7) of each leg branch is the shortest, and does not taper (Pl. 21, fig. 1; Pl. 22, figs. 1, 2; see also Whittington 1975, pl. 5, fig. 1; pl. 7, figs. 1, 3; pl. 18, fig. 2; pl. 24, fig. 4). Into the tip are inserted three spines, a large median and two lateral, each bluntly tapering, with the tip a sharp point. These spines are preserved turned inwards, in lateral view in 34694 (text-fig. 5; Pl. 21, fig. 1); in ventral aspect, extended, in 34695 (text-fig. 6; Pl. 22, figs. 1, 2). Presumably they were movable; there was ample space in podomere 7 for muscles attached to them, and they were an aid to digging when the limb was flexed.

The morphology of the coxa and leg branch is consistent, therefore, with *O. serratus* having been a benthonic predator, able to dig in search of prey, as well as for concealment. The activities by which it hunted for food are considered in the next section.

THE ACTIVITY OF *OLENOIDES SERRATUS* AND POSSIBLE RESULTANT TRACE FOSSILS

Walking. The basic limb movements employed in walking by Recent arthropods in which the leg is longer than the sagittal length of the segment, are explained by Manton (1977, pp. 39–49). The suggested manner in which *O. serratus* walked (Whittington 1975, pp. 129–131, figs. 25–28) was based on this work. Text-fig. 10 is an attempt to clarify the action of the coxa and leg branch in such walking, by showing four stages in the promotor-remotor swing, about an approximately horizonal, transverse axis at the coxa-body junction. The action of supposed intrinsic leg muscles is shown, in varying the length of the leg, keeping the tip firmly on the substrate, and giving the propulsive force. The muscles extrinsic to the coxa, which effected the promotor-remotor swing, are not shown. Each pair of legs moved in unison, and it is essential for effective walking that the tip of the limb be kept firmly in one spot during the remotor swing. It is because of this that the length of the leg, as measured in a straight line from axis of swing to tip of limb (Manton 1977, fig. 2.3), changes during the remotor swing, the leg extending (text-fig. 10, limb V) as the tip is put down, flexing (text-fig. 10, limb VII) as it moves into the vertical plane through the axis, and extending (text-fig. 10, limb IX) as the limb swings back behind this plane. There may have been eight legs in each metachronal wave of movement, legs V–IX in text-fig. 10 (in which legs VI and VIII are omitted) propulsive on the sea bottom, legs II–IV in text-fig. 10 (in which legs II and IV are omitted) swinging forwards in the recovery phase. A series of 'stills' in this gait are depicted in text-fig. 11, together with their relation to the trackway. The body is well supported in this slow movement close to the ground, each leg in a curve convex upwards which gives a hanging stance (Manton 1977, p. 200, fig. 5.1). In *O. serratus*, legs III to XI are of similar size, legs I, II, XII–XV being shorter. Thus the track made in this gait (text-fig. 11 and Whittington 1975, fig. 28) consists of a parallel series of overlapping footprints of legs III to XI, with footprints of legs I, II, XII, and XIII slightly closer to the midline. In text-fig. 11 the imprints of legs XIV and XV, which would have been successively slightly closer to the midline than those of legs XII and XIII, are not shown for simplicity; in such gaits the shorter limbs may not always make contact with the bottom. If the gait had been slightly different, for example in the phase difference between successive leg movements, or in the duration of forward and back strokes, the number of legs in a metachronal wave would have been different, but the track would remain essentially similar. That is, it would consist of two parallel overlapping series of prints, and at intervals, a pattern of imprints inside the parallel series. Only the nature of the inside pattern would vary slightly with small changes in gait. It will be appreciated that the neat, round footprints of text-fig. 11 are idealized; when walking in soft sediment the print would have been less neat, and may have been elaborated with additional lines, curved forwards and outwards, as the tip of the limb was withdrawn and swung forwards.



TEXT-FIG. 10. Oblique diagram of *Olenoides serratus* to show promotor–remotor swing of coxa and leg branch in walking, together with supposed joints between podomeres and action of intrinsic muscles. Right coxa and leg branch III, V, VII, and IX are shown, in positions corresponding to those in text-fig. 11*c*. Limb III has been lifted off the ground by levator muscles, extended by hydrostatic pressure, and is half-way through the promotor swing about axis A. Limb V, extended at the beginning of the remotor swing, has tip of limb held firmly on sediment by action of depressor muscles on podomeres 2 and 3, and action of flexor muscles on podomeres 4–7 gives propulsive force to body. Limb VII has reached mid-point of remotor swing, and lies in the vertical transverse plane through the axis of swing (A). Action of flexor muscles has given propulsive force and flexed leg to accommodate to reduced length, depressor muscles have kept tip of limb firmly on sediment. Limb IX is extended at the end of the remotor swing, the depressor muscles have given the propulsive force and kept tip of the limb on the sediment, the flexor muscles relax and allow podomeres 4–7 to become aligned and extend the limb. Black circles show position of joints; dashed lines show portion of podomere which inserts into coxa or podomere proximal to it; curved arrows show amount of rotation about axis; straight arrows show direction of pull of muscles.

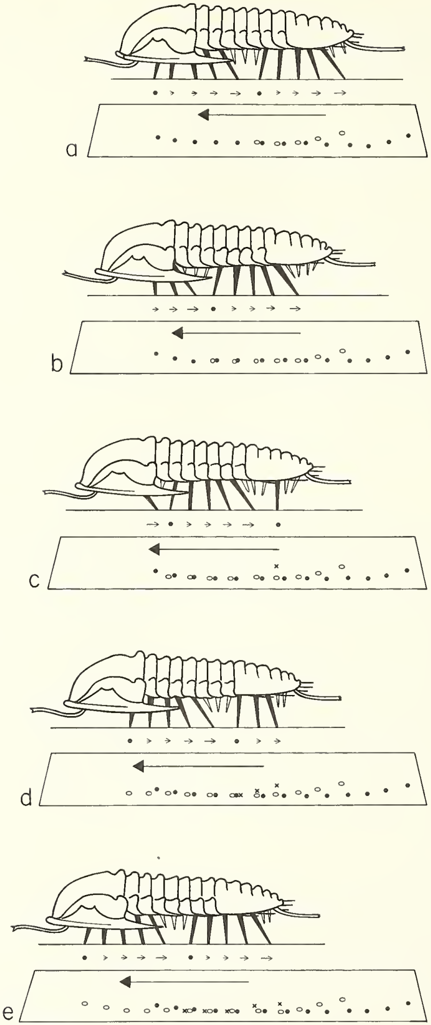
Seilacher (1955, text-fig. 1*b*, *c*, *d*) illustrated what he regarded as forward walking tracks of trilobites, and offered an interpretation (1955, p. 346, text-fig. 1*a*) of how they were made. It requires that the pairs of legs be longest anteriorly, diminishing in length progressively backwards, that only the anterior seven to nine pairs of limbs were used in walking, and that the pairs moved in opposite phase. In *O. serratus* (text-figs. 9–11) it is here assumed that the promotor–remotor swing of a pair of limbs in unison was used in walking and to macerate food and carry it forwards to the mouth. Dr. S. M. Manton pointed out (pers. comm.) that only for special reasons in certain groups of Recent arthropods is a pair of legs moved sometimes in the same phase, and at other times in an opposite manner. Thus I regard Seilacher's interpretation as inherently an unlikely manner of walking for any trilobite. It is possible, however, that the tracks, illustrated by Seilacher (1955, pl. 16, fig. 3; text-fig. 1*b*, *c*, *d*) were made by an arthropod walking in the manner here suggested, the outward and forwardly directed impressions being made as the limbs were withdrawn. This possibility requires further investigation. Seilacher (1955, text-fig. 1*e*,*f*) used the manner of walking he proposed in the interpretation of another track as that of oblique walking. In this he has been followed by Osgood (1970, p. 352, text-figs. 17*b*, 20*a*, etc.). Such tracks should be re-examined, and the interpretation reassessed.

A different Lower Cambrian track was regarded by Seilacher (1959, pp. 390–391, fig. 2*b*) as made by a trilobite walking forwards. It consists of a closely spaced repetition of eleven or twelve paired imprints arranged in a 'V' opening forwards, and having a pair of grooves between the imprints at the base of the 'V' (the left half is shown in the text-fig. 12). Seilacher suggested that eleven or twelve pairs of limbs only were used in walking, the series moving in a single metachronal wave at one time. Text-fig. 12 is an attempt to fit this manner of progress to the track, using the trilobite drawn by Seilacher. The appearance is improbably unstable, and Dr. S. M. Manton informed me (pers. comm.) that she knew of no Recent arthropod that when walking had one metachronal wave of limb movement upon the limb series at one time. In locomotory mechanisms considered by Manton (1977, pp. 293–331) every device is used to keep the number of supporting legs as even as possible, i.e. to keep the load on each leg similar (cf. text-fig. 11). I conclude that the way in which this track was made requires reassessment.

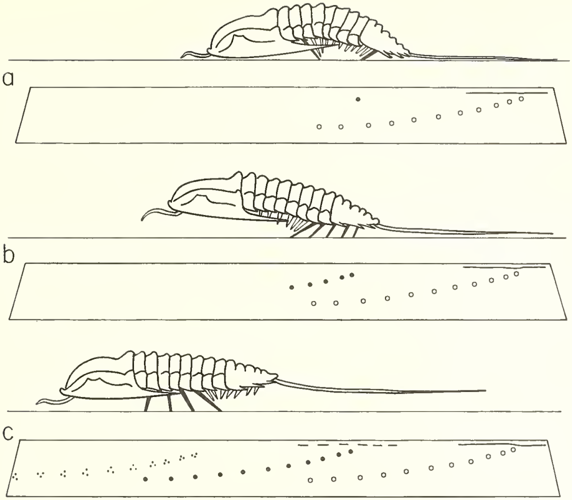
The further suggestion (Seilacher 1939, p. 391; Osgood 1970, pp. 351–352; 1975, p. 98) that in rapid walking only the longer, stronger, anterior legs of a trilobite were used, and that the hinder portion of the animal was supported, sliding along on the cerci or pygidial border spines, is also improbable. At any speed of walking, dragging part of the body is a hindrance, and the speed of walking does not depend on the supposed strength of longer legs, but on the pattern of the gait (Manton 1977, pp. 298–308). The lateral bristles on the cerci of *O. serratus* (Pl. 21, fig. 1) do not suggest that the cerci were adapted to slide on.

Jumping off the sea bottom. An undescribed trace fossil, showing a series of paired imprints repeated at intervals, led Manton (1977, p. 48) to refer to the possibility of a trilobite using a few successive limb pairs to launch itself off the bottom and drift or swim before sinking down again. Text-fig. 13 shows this activity of the thoracic limbs (which are similar in length), and the resulting tracks. In the back stroke the limb movements are not synchronous, but in a wave with a slight phase difference between each successive leg. Thus limb pair X end the backstroke and are the first to leave the bottom, and pair IV are the last. On landing, pair X have completed the forward swing and touch down first, followed in rapid succession by pairs IX to IV. Pair X begin the remotor swing first, and the limbs move in succession into the positions shown in text-fig. 13*a* for the next jump. In a favourable current this appears a plausible mode of progression for *O. serratus*, which probably had feeble swimming powers. The distance between the parallel sets of paired impressions (text-fig. 13*c*) would have depended on the strength of the jump, on the swimming powers, and the direction and strength of any current; many variations on the simple pattern of text-fig. 13 may have occurred. The track shown in text-fig. 12 is a repetitive pattern, involving far more pairs of limbs than that of text-fig. 13. To fit the trilobite shown in text-fig. 12 to the track, when progressing in short jumps, is difficult, requiring not only a wide angle of swing of the legs, but also that the posterior pairs be long and steeply inclined. It does not appear a plausible interpretation of this track.

Digging and furrowing. It is reasonable to suggest that in hunting for small, mainly soft-bodied animals, and in scavenging, *O. serratus* dug into the substrate. Such digging could have been effected by flexure and extension of pairs of limbs along the body, the leg branches directed outwards, with a slight fanning anteriorly and posteriorly (text-fig. 14). The promotor–remotor swing of the limbs is not involved in this activity; at the late Dr. Manton's suggestion I portray flexure and extension of alternate pairs of limbs. The excavation so made would have been bilobed, and some of the transverse grooves dug during flexure might be visible. It is possible that if the animal dug sufficiently deeply, and if it rested in the excavation (in part for concealment), the impressions of the ventral margins of the exoskeleton, including spines, and even of the limbs themselves, might be preserved.



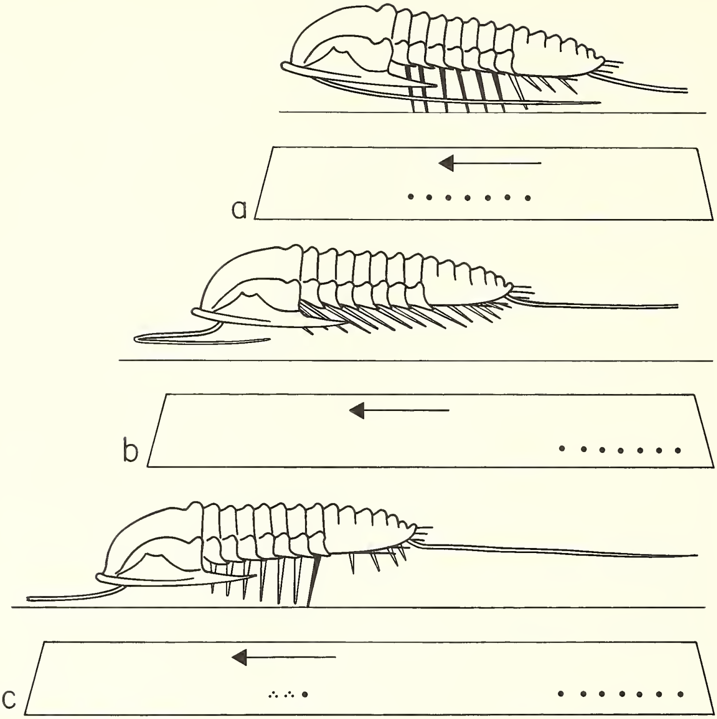
TEXT-FIG. 11. See explanation on p. 197.



TEXT-FIG. 12. A most improbable mode of progression for a trilobite, suggested to explain a particular track. The left half of the symmetrical track (after Seilacher 1959, fig. 2*b*) is shown in oblique lateral view, below each 'still' of the trilobite progressing forwards in the manner suggested by Seilacher (1959, pp. 390–391). Legs XVII to VII are supposed to have been used in successive pairs, in a single wave of motion which proceeded forwards along the body.

a, open circles show track of preceding wave, limb VII at end of remotor swing resting in anterior print of this track. Body flexed to bring limb XVII forwards to begin first print (solid circle) of next wave. Pygidium flexed down and cercus makes impression between posterior prints of preceding wave. *b*, limbs XVII to XIII are put down successively and begin remotor swing. Cercus lifts off bottom. *c*, Limbs XVII to XI complete remotor swing, lift off, and are shown in stages of promotor swing. Limbs X to VII on sea bottom, in stages of remotor swing, complete the set of impressions. Position of next set shown by stipple, which will begin as limb VII completes remotor swing and body flexes (*a*). The trilobite shown is like that depicted by Seilacher, legs in contact with sea bottom shown in solid black, those off the bottom in outline.

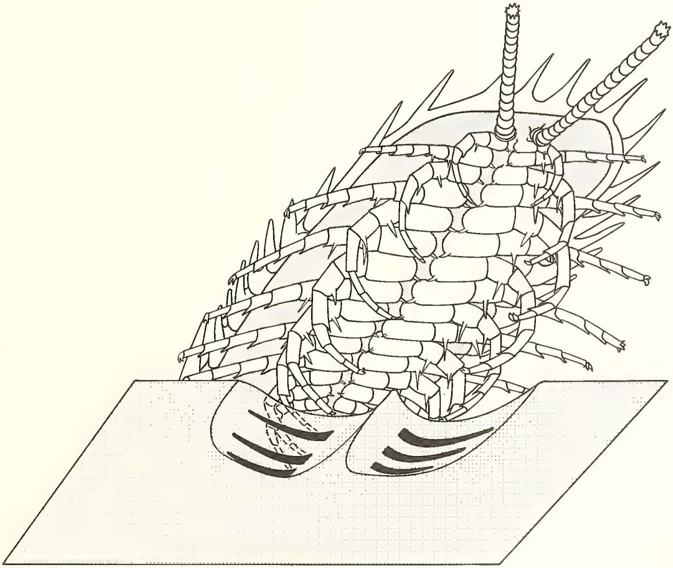
TEXT-FIG. 11. How a trilobite probably walked. Left lateral 'stills' of progression of *Olenoides serratus* in the possible gait described in Whittington 1975, pp. 129–131, figs. 25, 26E, 27 (cf. Manton 1977, fig. 2.5). *a–e* are successive stages, progressing in the direction shown by the large arrow, which lies in the sagittal plane. Each metachronal wave of eight leg pairs passes forwards along the body. Thirteen pairs of legs are shown being used in this gait (i.e. the last two pairs are not used). Each selected still-stand shows left legs only, in solid black when in contact with the sea bottom, in outline when off the bottom and swinging forwards. Respectively: *a*, legs I–V in first wave, VI–XIII in second wave; *b*, legs I–III in first wave, IV–XI in second wave, XII, XIII in third wave. *c*, leg I in first wave, legs II–IX in second wave (legs II and III are off the bottom and concealed beneath the cephalon), legs X–XIII continuing the third wave; *d*, legs I–VII (legs I and II concealed) in second wave, VIII–XIII in third wave; *e*, legs I–V in second wave, VI–XIII in third wave. Below tip of each limb on bottom is either a solid circle, showing limb tip has just been put down, or an arrow of length proportional to amount of backstroke completed. The panel below each 'still' shows in oblique lateral view the left half of the symmetrical track made in this gait, solid circles are footfalls of first wave affecting legs I–V in *a*, open circles footfalls of second wave, crosses (*c*, *d*, *e*) footfalls of third wave. Antenna and cercus incomplete.



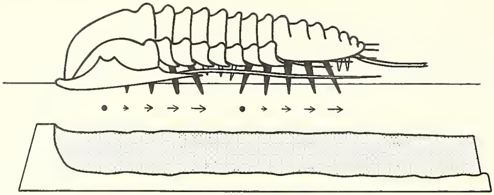
TEXT-FIG. 13. Left lateral 'stills' of how *Olenoides serratus* may have launched itself off the sea bottom to drift or swim a short distance before descending to the bottom (cf. Manton 1977, p. 48). *a*, leg pairs IV to X swung back quickly launches animal, imprint of left legs shown in oblique lateral view in panel below. *b*, animal drifts or swims, pairs of legs swung back to offer less resistance. *c*, leg pairs IV–X in promotor swing, pair X complete swing and touch bottom, to be followed in succession by pairs IX to IV, giving a second set of impressions. Antenna incomplete, cercus complete in *c*. Limbs in solid black in contact with sea bottom, arrow in sagittal plane of animal shows direction of movement.

Such traces have long been known as *Rusophycus* (Crimes 1970 and references; Osgood 1970, pp. 301–308), and Crimes (1975) and Baldwin (1977) have argued that these excavations were cast in sand or silt at the sediment–water interface. Not all bilobed excavations were the work of trilobites (e.g. Osgood 1970, pp. 303–304), but those showing impressions of the exoskeleton or of limbs, appear indubitably so. Osgood (1970, p. 304, pl. 57, fig. 6; pl. 58, figs. 4, 5) also refers to three specimens of *Rusophycus*, in one of which the exoskeleton of the trilobite *Flexicalymene meeki* lies upon the cast of an excavation. He regards the specimens as proving that the excavation was made by a trilobite. However, if one accepts the explanation by Crimes (1975, pp. 41–47) that the excavation was dug and subsequently cast in sand or silt, I have difficulty in understanding how the exoskeleton comes to lie 'in place' above the cast. Despite the doubts and difficulties in interpreting specimens of *Rusophycus*, it does appear possible that digging by *O. serratus* in search of prey or for concealment (text-fig. 14), could have resulted in a *Rusophycus* type of trace. Indeed, both Martinsson (1965, p. 211) and Bergström (1973, p. 54) have argued that such traces were made in hunting.

It may also be reasonable to suggest (cf. Manton 1977, p. 48) that *O. serratus* could have ploughed shallowly in loose, wet sediment in search of food. This could have been achieved using the normal walk (text-fig. 11), but with the cephalon inclined downwards and presumably the antennae swung back outside the limbs (text-fig. 15). Such an activity would have produced a shallow furrow approximating to the width of the cephalon. The footfalls would have been at the margin of the furrow, and hardly likely to be preserved in wet sediment which may have slipped at the edge of the furrow. Such a nondescript trace would not attract attention. A different type of furrow, however,

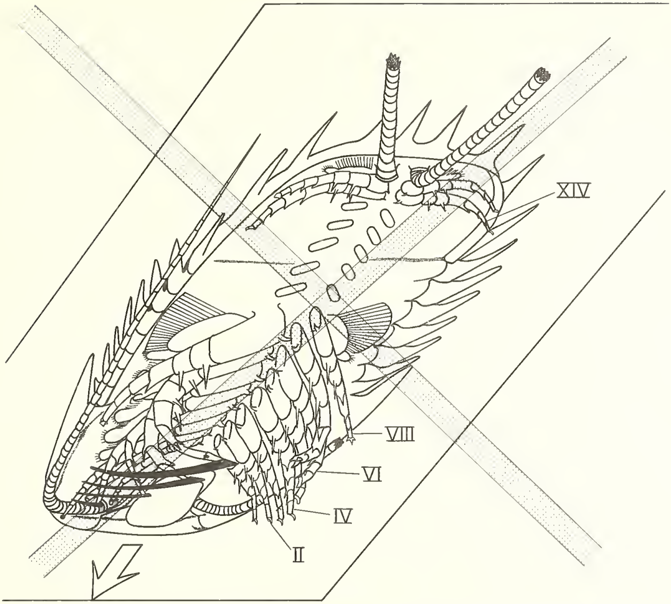


TEXT-FIG. 14. Diagrammatic oblique ventral 'still' of *Olenoides serratus* alternately flexing and extending pairs of limbs. Coxae and leg branches I to XV and their major ventral spines are shown, gill branches omitted. During flexure the limbs dug into the sediment and excavated a shallow depression. Lower part of drawing shows surface of sediment (stippled) from below, including that part of the bilobed excavation below the first seven pairs of appendages. The grooves in the excavation made by the flexure of limb pairs I, III, and V are shown in black and on the left side dashed lines show the concealed distal portions of these limbs. Antennae assumed to be forwardly extended, cerci incomplete. Ventral cuticle stippled.



TEXT-FIG. 15. Left lateral 'still' of *Olenoides serratus* in gait shown in text-fig. 11, but with cephalon inclined downwards and ploughing shallowly into sediment. Horizontal line shows position of sediment surface, antennae curved back, left half of furrow shown in oblique lateral view in panel below. Other symbols as text-fig. 11.

has long been remarked upon. This is the trace fossil *Cruziana*, which has been interpreted confidently as resulting from the activity of trilobites (e.g. Seilacher 1970; Crimes 1970, 1975; Birkenmajer and Bruton 1971). This trail, observed extending straight or slightly curved for a metre or more, is a bilobed furrow reaching 5–6 cm in width, each furrow showing diagonal grooves forming a V-pattern, and it has been widely agreed that the grooves diverge forwards. If such a trail was made by *O. serratus*, it should be possible to propose appropriate limb movements by which it was made, and to give a reason for this activity; I have found it impossible to do either in a plausible manner. To take limb movements first: in contrast to those shown in text-fig. 14, these movements would have to have provided forward propulsion of the animal, combined with diagonal digging. Without serious thought, I earlier (1975, p. 131) suggested that in *O. serratus* a combination of a remotor swing of the limb with flexure would give diagonal scratches. The previous section has shown that flexure of the limb was confined within the antero-posteriorly flattened plane of coxa and leg branch, because of the medial position of the pivot joints and the alignment of the hinge joints along the dorsal margin (text-fig. 10). To attain an inward and backward movement of the tip, the limb would have to have been flexed, and at the same time swung back about the horizontal axis (A in text-fig. 10). In such a postulated action, the intrinsic leg muscles would have acted to dig a groove, but the only forwardly propulsive force to the body would have to have come from the extrinsic muscles in the remotor swing. Given the nature of the coxa–body junction, narrow and with no articulation. I doubt that there would have been sufficient force to drive the body forwards, even if the limb series were to have been acting in metachronal waves. Text-fig. 16 shows movements of limbs in pairs which could have dug grooves directed inwards and backwards, and may at the same time have given a variable and uneven drag forwards to the animal. If each limb was swung at the coxa–body junction, about a vertical axis, into an outward and forward-directed position, then as the leg flexed it would have dug a groove inwards. The limb is suggested to have been directed in this manner, in order that if there were resistance to digging, then the animal would have been dragged forwards as the groove was cut. Text-fig. 16 suggests that the limbs may have worked in a metachronal wave of six, and shows limb pairs III to VII in successive stages of digging a groove, with limb pair VIII extended off the ground after completing the digging action. Limb pairs I, II, XIV, and XV are shown as not taking part in the digging, and are extended above the sea bottom. The track of the groove dug by a limb is a resultant of inward digging and forward progress. If the sediment in which the animal was digging was so wet as to offer no resistance, a straight groove would have been dug, and there would have been no forward progress. If resistance were offered, the groove would have been curved, the amount of curvature determined by the resultant forward progress. If resistance varied between one side and the other, the direction of movement would have been shifted. Successive waves would have formed an over-



TEXT-FIG. 16. A highly improbable mode of progression for a trilobite. Diagrammatic oblique ventral 'still' of *Olenoides serratus*, limb pairs I to XIII swung into a forward and outward direction, pairs III to VIII in stages of a metachronal wave of flexure and extension. It is assumed that limb pairs I, II, XIV, and XV did not take part in the movement, remaining extended; limb pairs IX to XIII not shown for simplicity, gill branches lying beneath the ventral cuticle, antennae curved back beside body, cerci incomplete. As each limb was flexed it would dig a groove; these grooves are shown beneath the left side only, for simplicity. Arrow suggests direction in which animal may have been dragged forwards by digging action.

lapping series of grooves varying in direction and curvature (not symmetrical), typical characters of *Cruziana* (cf. Birkenmajer and Bruton 1971, fig. 10). A metachronal rhythm of the type suggested may have given a more or less continuous forward push, and have maintained the body in a roughly horizontal position, supported along its length. The lateral border and genal spine may have made a lateral groove, and the movement of the curved-back antenna a smoother zone inside the groove (Crimes 1975, fig. 1). The gill branches would have lain beneath the ventral cuticle (text-fig. 16), protected by the pleural regions, and could not have assisted in excavation. For this activity to have been effective, the coxa and leg branch would have to have been held at a fixed angle (45° to the sagittal line is chosen in text-fig. 16). This activity may appear plausible at first glance, but the late Dr. Manton regarded it as highly unlikely, advising me against publication of text-fig. 16 because it was so misleading. I disregard her advice with considerable hesitation, and superimpose a cross on the figure. There are two major considerations that make this activity unlikely:

(1) as a method of seeking food it is slow, clumsy, and inefficient. With the limbs in the position shown, opposing pairs cannot have been flexed to grasp prey efficiently with the numerous spines, as they could in the *Rusophycus* type of activity (text-fig. 14). That is, if the animal had encountered a small worm or other prey, it would have had to swing the limbs outwards into the transverse plane to seize it, and also to begin the promotor–remotor movements which would have enabled it to tear up the food and convey it forwards to the mouth. Far more efficient would have been for the animal to have sought food by walking (text-fig. 11) or ploughing (text-fig 15) shallowly over the sea bottom, and on detecting it to have dug down and seized it between the flexed limbs (text-fig. 14).

(2) Dr. S. M. Manton, who has recorded the walking trails made under water by many Recent marine arthropods, assures me that no comparable trail is known. That is, no living arthropod is known to progress forwards by such limb movements; in locomotion the tip of the limb is kept on one spot during the propulsive stroke.

I conclude that *O. serratus* did not behave in the manner portrayed in text-fig. 16, and can devise no plausible way by which it could have made the *Cruziana* type of trace. The arguments by which *Cruziana* is attributed to trilobites (e.g. Seilacher 1970, pp. 448–449) are not conclusive, and discussions of how the trace was made (e.g. Birkenmajer and Bruton 1970, pp. 313–317; Crimes 1970, pp. 51, 61–65; 1975, pp. 36–37; Seilacher 1970, pp. 449–452) are vague and unsatisfactory, particularly in not explaining how forward progression combined with excavation was accomplished. The origin of this trace is an unsolved problem, as is the question of any relationship between the *Cruziana* and *Rusophycus* types of traces. In the Middle Cambrian Burgess Shale fauna, kinds of non-trilobite arthropods outnumber trilobites by at least two to one. Perhaps the *Cruziana* trace was made by a non-trilobite arthropod, or even by some animal other than an arthropod.

Sideways raking. Traces which include groups of parallel scratches have been attributed to trilobites (Osgood 1975, pp. 98–100, and references). These include the celebrated sideways raking described by Seilacher (1955, pp. 349–355, pl. 17, fig. 2, text-fig. 3), in which the activity of the appendages in making the track is portrayed. The legs of one side are shown as flexing and extending, in a wave of motion which moved forwards along the body, while the tips of the extended legs of the other side acted as rakes as the animal moved sideways. This appears at first glance as a plausible activity for *O. serratus* (cf. Whittington 1975, p. 131, fig. 29). Seilacher interpreted the raking activity as for feeding, systematically stirring up food particles, which were filtered by the gill branches and carried to the mouth by currents resulting from the limb movements. I consider this mechanism for food transport as improbable, and regard *O. serratus* as not a filter feeder. Sideways raking as a method of hunting seems less efficient than walking or shallow ploughing, and thus an unlikely activity for *O. serratus*. Other criticisms of interpretations of raking trails are mentioned by Osgood (1975).

Activity of other trilobites. My conclusions on the mode of life of a second trilobite from the Burgess Shale, the unique *Naraoia compacta* (Whittington 1977, pp. 436–439), are like those on *O. serratus*, as modified and expanded here. *N. compacta* possessed an exceptionally powerful apparatus for seizing and macerating food, and the single articulation in the thorax was apparently an adaptation well suited to shallow ploughing of the type shown in text-fig. 15. Most probably it behaved much as *O. serratus* may have done (text-figs. 11, 13, 14) in walking, jumping, and drifting, and in digging, but I now regard sideways raking as unlikely and the making of the *Cruziana*-like furrow as an improbable activity for *N. compacta*.

Appendages are also known in one species each of *Ceraurus* (Størmer 1939, 1951), *Phacops* (Seilacher 1962; Stürmer and Bergström 1973), *Triarthrus* (Cisne 1975), and *Cryptolithus* (Campbell 1975, fig. 13), which range in age from Ordovician to Devonian. In each, the series of limbs is graded in length, shorter anteriorly, of similar length from the last somite of the cephalon to posteriorly in the thorax, then a rapid diminution in the pygidium. I consider that the manner of walking in all these species was like that in text-fig. 11 (resulting in a track of that type), and not like either of the ways suggested by Seilacher (1955, fig. 1*a*; 1959, fig. 2*b* and text-fig. 12). The interpretation of certain tracks by Seilacher (1955) and Osgood (1970) therefore requires re-examination. I consider it unlikely that trilobites normally walked using only a few anterior pairs of limbs, and that the pygidium was dragged along. These species have all been interpreted as filter feeders, except *Phacops* (Stürmer and Bergström 1973, pp. 118–120), considered both a predator and filter feeder. I am not persuaded by the arguments advanced for filter feeding, but if this were the habit, then presumably sideways raking was a possible activity. Shallow ploughing (text-fig. 15), jumping and drifting (text-fig. 13), and digging (text-fig. 14) for concealment if not in hunting, are likely activities. For the reasons given in the previous section, I am doubtful that *Cruziana* should be attributed to trilobites, so that text-fig. 16 represents a most unlikely activity for any of these species.

Acknowledgements. In 1966 and 1967 a reinvestigation of the Burgess Shale (Whittington 1971; Fritz 1971) was undertaken by the Geological Survey of Canada, with the co-operation of authorities of the Yoho National Park and Parks Canada, Department of Indian and Northern Affairs, Ottawa. The Geological Survey of Canada kindly invited me to be Chairman of the palaeobiological work, and I am indebted to the Natural Environment Research Council (grant GR3/285) for support of both field and laboratory work. Every facility for study of the Walcott collection in the National Museum of Natural History (formerly U.S. National Museum), Washington, D.C., was afforded by Drs. Porter M. Kier and Richard E. Grant. My photographs have been enlarged by Mr. David Bursill and Mr. John Lewis has skilfully converted my pencil drawings into the present figures. My debt to the late Dr. S. M. Manton, F.R.S., for discussion and advice in the course of this work, is evident. Dr. D. E. G. Briggs found the specimen which on preparation proved to be a second example of '*N. transitans*'; both he and Dr. C. P. Hughes made helpful comments as my ideas developed. Dr. J. V. P. Long kindly made the analyses of the exoskeletal layer.

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TRICHOTHYRIACEOUS FUNGI FROM THE EARLY TERTIARY OF SOUTHERN ENGLAND

by PETER H. SMITH

ABSTRACT. Isolated ascocarps (thyriothecia) from Upper Eocene deposits of the Hampshire Basin are described as a new species of the genus *Trichothyrites* Rosendahl within the Trichothyriaceae, a family of epiphyllous fungi not previously recorded from English Tertiary deposits. Comparisons are made between the fossil material and the extant genus *Trichothyrina* Petrak to establish their affinity. Earlier records of epiphyllous fossil fungi from British deposits are reconsidered in view of recent taxonomic changes in living taxa.

IN the course of an examination of fungal material from the Leaf Bed (Bed X of Tawney and Keeping 1883), of the Lower Headon deposits (Upper Eocene/Lower Oligocene) from Hordle Cliff, Hampshire, thyriothecia ascribable to the Trichothyriaceae have been recognized (see Smith 1978 for grid reference and methods of isolation). Examples of this type of fructification have not previously been described from deposits earlier than Quaternary in Britain.

Although ascomycetous fungi have been shown to be present in fossil deposits of Upper Carboniferous age (Batra *et al.* 1964) it is interesting to note that the majority of fossil epiphyllous ascomycete forms are reported only from Tertiary deposits. As shown by Tiffney and Barghoorn (1974) the bulk of Tertiary ascomycetes are epiphyllous forms occurring in association with leaf cuticles. Graham (1962) attributes this to rapid adaptive radiation of the ascomycetes to capitalize on the vast expansion of potential habitats within the phyllosphere following the appearance of the angiosperms. However, as Tiffney and Barghoorn caution, this apparent rapid diversification and numerical increase in fossil forms may in part be due to the large number of palaeobotanical investigations made upon leaf bed deposits from the Tertiary. Apart from the epiphyllous fungi from the Lower Cretaceous flora described by Krassilov (1967), there is little published evidence to suggest that a diverse epiphyllous fungal flora existed prior to the Tertiary. This could well be due to the fungal element being overlooked or disregarded as not worthy of further investigation by workers concentrating on the leaves themselves.

The presence of fructifications of epiphyllous fungi in Tertiary fossil deposits has generally been accepted as indicating warm sub-tropical to tropical climatic conditions, in light of the predominantly tropical distribution of extant taxa of the Microthyriales. This contention is reinforced by the comparative work on fossil and extant forms of epiphyllous fungi of Lange (1976, 1978) from the Southern Hemisphere.

TAXONOMIC CONSIDERATIONS

Considerable recent advances have been made in the understanding of the taxonomic relationships of extant taxa (Müller and von Arx 1962; Luttrell 1973). Few workers interested in fossil forms have had these modern treatments available for consultation, and have often tended to use 'microthyriaceous' in an all-embracing term. Records of British fossil epiphyllous fungi can now be ordered as follows (see Table 1) using the classification of Luttrell (1973). Godwin and Andrew (1951) reported the common occurrence of *Microthyrium*-like thyriothecia (with a tentative affinity with *Loranthomyces* von Höhnel of the Trichothyriaceae) in Post-Glacial peat deposits ranging from the Pennines to Somerset. Vishnu-Mittre (1973) attributed thyriothecia from Flandrian peat deposits at Whittlesey Mere to two extant species, *M. culmigenum* Sydow and *M. nigro-annulatum*

[Palaeontology, Vol. 23, Part 1, 1980, pp. 205–212.]

TABLE 1

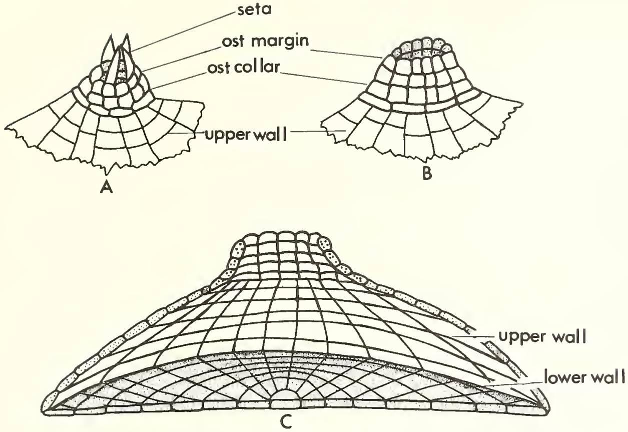
Class Loculoascomycetes

ORDER: MICROTHYRIALES	ORDER: DOTHIDEALES
FAMILY: MICROTHYRIACEAE	FAMILY: TRICHOTHYRIACEAE
	Microthyrium-like cf. *Loranthomyces* von Höhnel, 1917 (Godwin and Andrew 1951)
Microthyrium culmigenum Sydow, 1921 → (From Vishnu-Mittre 1973)	*Trichothyrina alpestris* (Sacc.) Petrak, 1950 (From Ellis 1977)
Microthyrium nigro-annulatum Webster, 1952 → (From Vishnu-Mittre 1973)	*Trichothyrina nigro-annulata* (Webst.) Ellis, 1977 (From Ellis 1977)
*Phragmothyrites** *eocenica* Edwards, 1927	
*Phragmothyrites** *hibernica* Johnson, 1949	
FAMILY: MICROPELTIDACEAE	
*Stomiopeltites** *cretacea* Alvin and Muir, 1970	

* Denotes fossil genus.

Webster, and commented upon the similarity of the material to that described by Godwin and Andrew. Ellis (1977), however, in her critical taxonomic review of extant British Microthyriaceae, has removed the species cited by Vishnu-Mittre both from the genus *Microthyrium* and the family Microthyriaceae (see Table 1). Based largely upon differences in thyriothecial construction, both species have been placed in the genus *Trichothyrina* Petrak in the family Trichothyriaceae. These are the only Dothidealian fungi in the fossil record from Britain. Microthyrialian fungi are only slightly better documented. Alvin and Muir (1970) erected the genus *Stomiopeltites* for fructifications resembling those of *Stomiopeltis* Theissen from the family Micropeltidaceae. These fossil forms were borne on leafy conifer shoots from the Lower Cretaceous deposits of the English Wealden. Edwards (1922) described *Phragmothrites eocenica* based on fructifications borne on conifer leaves of Eocene age from Mull, Scotland, whilst Johnson (1949) described *P. hibernica* on cuticles attributed to *Fagus* from an Eocene deposit of Ireland.

Selkirk (1975) has enumerated the difficulties involved in positive identification of thyriothecia from fossil deposits as members of the Trichothyriaceae, rather than Microthyriaceae the uncertainties involved being centred upon details of thyriothecial construction. These concern the ostiole borne on a short papilla of thickened cells often, but not always, bearing setae on the uppermost ring of ostiolar collar cells (see text-fig. 1A and B), and the cellular pattern and construction of the thyriothecium. In contrast to the dimidiate construction of fructifications of Microthyriaceae where the lower wall is extremely thin and delicate, those of Trichothyriaceae are complete with well-developed upper and lower walls, each composed of radiate files of cells which appear almost isodiametric in surface view (see text-fig. 1C). This pattern of cellular arrangement of quadrilateral cells is also present in the upper wall of the thyriothecia of Microthyriaceae close to the ostiole, but cells generally become more elongate towards the margins.



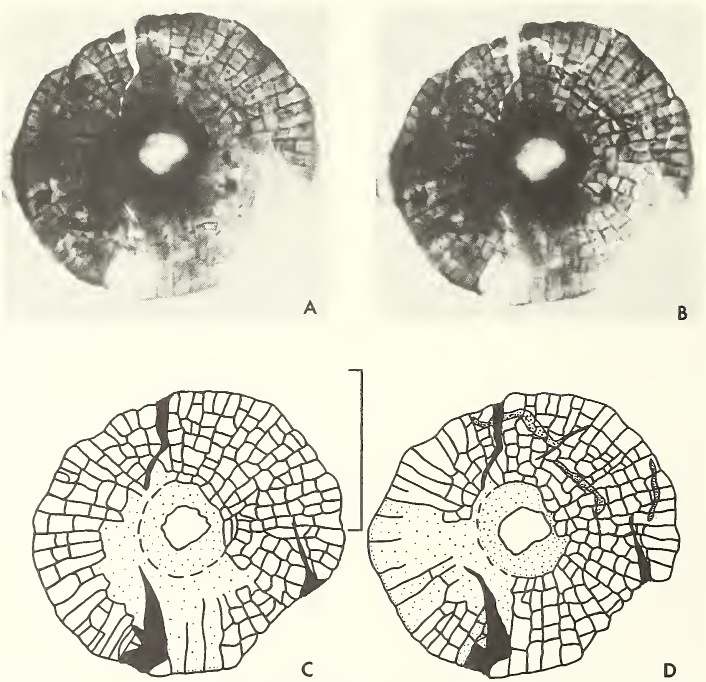
TEXT-FIG. 1. Diagrammatic representations of thyriothecium constructions in Trichothyriaceae. A, ostiole bearing setae on ostiolar margin. B, ostiole with smooth ostiolar margin. C, vertical section of the thyriothecium showing 3D structure. ost = ostiolar.

Microscopic examination of the Hordle Cliff thyriothecia has resulted in the recognition of several criteria that it is felt allow accurate assignment of the fructifications as those of Trichothyriaceae. The papilla bearing the ostiole has retained sufficient height in the fossils to remain a distinguishing feature. Despite dorsiventral compression of the entire fructification the thickened cells of the papilla usually remain erect and thus the terminal ostiole is observable in a higher focal plane than the cells of the upper wall of the fructification. Compression of the fructification and subsequent preparation treatment often leads to rupture of the walls enabling the presence of a well-defined and complete lower wall to be seen (seen text-fig. 2).

Rosendahl (1943) used the features of a complete fossil thyriothecium (i.e. possessing both upper and lower walls), with an erect ostiolar collar and the marginal cells of the pore bearing setae, to describe *Trichothyrites pleistocaenica*. This species was found in association with both spruce needles and moss leaves from an early Pleistocene deposit from Minnesota. Those found on spruce needles were reported to be in close association with other fungal hyphae which were tentatively identified as a species of *Herpotrichia*. The relationship between these hyphae and the thyriothecia, however, remained problematic; no definite myco-parasitic relationship could be demonstrated. Mycoparasitism was further questioned on the grounds of the presence of apparently identical fructifications on moss leaves where no other fungal hyphae were demonstrable. Rosendahl therefore concluded that *T. pleistocaenica* was saprophytic, but no comparison was made with extant species. Since publication of Rosendahl's description, however, Petrak (1950) has elevated from subgeneric to generic level the taxon *Trichothyrina* for predominantly saprophytic fungi, as opposed to *Trichothyrium* Sacc. which is characterized as being a genus parasitizing other fungi. This would suggest that the closest affinity for *Trichothyrites* Rosendahl, would be this extant genus *Trichothyrina* Petrak. This is further borne out by an examination of the Hordle Cliff material. Here the thyriothecia are not associated with host material in most instances, but those that have been observed attached to cuticle are not in association with any other fungal hyphae, which would appear to preclude any suggested myco-parasitic relationship.

Size measurements used by Ellis (1977) in defining living species of *Trichothyrina*, would also suggest close affinity of the Hordle Cliff material with extant species. However, one of the major diagnostic features for separation of living species remains their mode of nutrition, a character impossible to ascertain with certainty in fossil material.

A number of fructifications of epiphyllous fungi from the Tertiary of the Southern Hemisphere and Lower Cretaceous of Siberia have been assigned to the genus *Notothyrites* (Cookson 1947; Selkirk 1975; Kemp 1978; Krassilov 1967). This genus bears a close resemblance to the material described here with the exceptions that no mention of a lower thyriothecial wall has been made in the descriptions nor shown in any of the specimens that have been figured. On these grounds *Notothyrites* has hitherto been considered as a genus of the Microthyriaceae. As no detailed comparison with the Southern Hemisphere material has yet been made it seems appropriate, at present, to retain *Trichothyrites* Rosendahl with an emended diagnosis allowing the incorporation of the Hordle Cliff material.



TEXT-FIG. 2. Construction of fossil thyriothecium. A and C, photographic and diagrammatic representation of upper thyriothecial wall. B and D, the same specimen at a lower depth of focus showing splits in upper wall and presence of lower wall. Scale bar = 50 μm.

SYSTEMATIC PALAEONTOLOGY

Genus TRICHOTHYRITES Rosendahl, 1943 emend.

Emended diagnosis. Thyriothecia appearing disc or saucer-shaped due to compression; possessing definite upper and lower walls of radiate rows of almost square cells (3–8 μm × 3–8 μm). Cell walls of upper layer of thyriothecium generally more strongly thickened than those of the lower layer. Thyriothecia ranging from 70 μm to 200 μm in diameter and bearing on upper wall an erect ostiolar collar (papilla) made up of from two to six tiers of small (2 μm × 2 μm) extremely thick-walled quadilateral cells. Uppermost tier (ostiolar margin) of cells may have short prolongations (setae) in some cases. Thyriothecial outline usually smooth but may appear lobate.

Type species. Trichothyrites pleistocaenica Rosendahl (1943), figs. 8–10, p. 132; figs. 18–20, p. 135.

Trichothyrites hordlensis sp. nov.

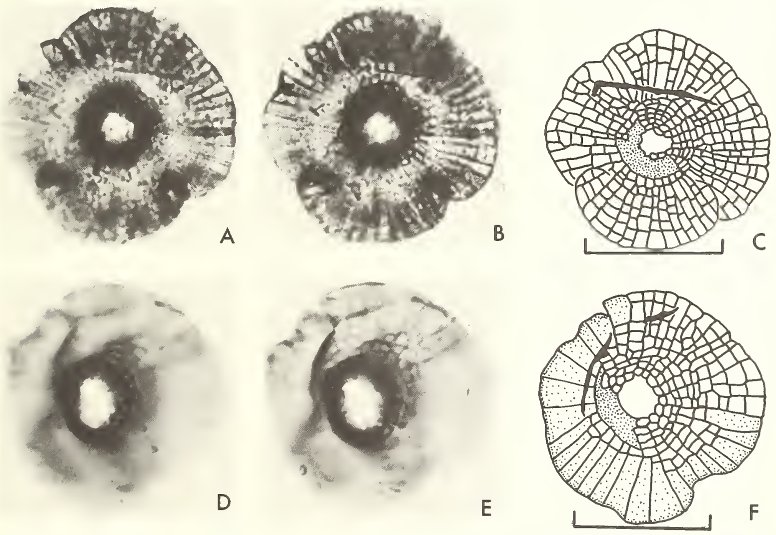
Text-fig. 3A–F

Holotype. Text-fig. 3A, B, and C, British Museum (Natural History), Department of Palaeontology slide no. V60215.

Type locality. Hordle Cliff, Hampshire (Grid ref. SZ262923).

Horizon. Hordle Leaf Bed (Upper Eocene/Lower Oligocene).

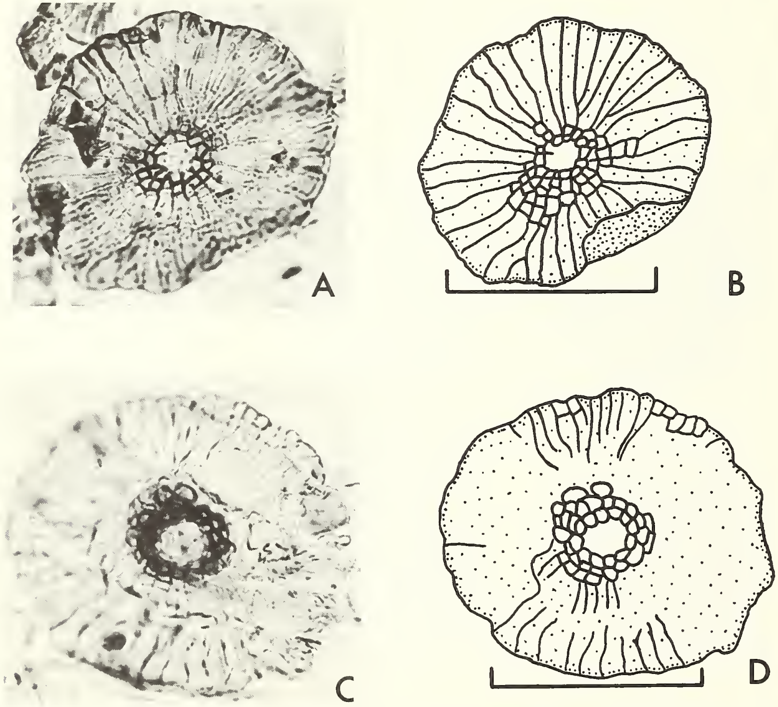
Diagnosis. Maximum diameter of thyriothecia 75 μm. Erect ostiolar collar of 3–4 tiers of small (2 μm × 2 μm) thick-walled quadrilateral cells, diameter of collar 20 μm; ostiolar marginal cells not produced into setae,



TEXT-FIG. 3. *Trichothyrites hordlensis.* A and B, fructifications at two focal planes showing thyriothecial construction especially upper wall. D and E, details of ostiolar region of *T. hordlensis.* C and F, interpretative drawings of specimens. Scale bar = 50 μm.

ostiolar pore diameter 10–15 μm. Upper wall of thyriothecium consisting of quadilateral cells arranged in rows radiating from ostiolar collar, cell size ranging from 3 μm × 3 μm near collar to 6 μm × 8 μm at margin. Cells of lower wall similar but with more delicate cell walls. Thyriothecia usually found as isolated structures not in association with cuticle or other fungal hyphae. Spores absent.

Discussion. The affinity of these fossil thyriothecia cannot be stated exactly as the final diagnostic character used for species determination by Ellis (1977) is the nature of the host substrate coupled with the shape of the ascopores. Although the large cells at the base of the ostiolar collar (see text-fig. 3A, B) may tend to suggest an affinity with *Trichothyrina alpestris* (Sacc.) Petrak, 1950, there is no clear indication that these cells are perforate in the fossil material. Similarly, although setal processes from the cells of the ostiolar may or may not be present in *T. alpestris*, their absence from the fossil material, coupled with the small over-all size of the fructification (75 μm v. 200 μm), small ostiolar collar diameter (20 μm v. 25–40 μm), all combine to suggest a closer affinity with *T. ammophilae* Ellis, 1977.



TEXT-FIG. 4. A, *Trichothyrites* sp. A. C, *Trichothyrites* sp. B. B and D, interpretative drawings. Scale bar = 50 μm.

Trichothyrites sp. A

Text-fig. 4A, B

Fructifications of this type are present in the Hordle Cliff material at a much lower frequency than those of *Trichothyrites hordlensis*. Insufficient numbers have been isolated so far to erect a detailed specific diagnosis but a tentative affinity with *Trichothyrina pinophylla* (von Hohn.) Petrak, 1950 is suggested due to the smaller number of tiers in the ostiolar collar and the much smaller (60 μm) overall diameter of the fructification.

Trichothyrites sp. B

Text-fig. 4C, D

Again, insufficient material precludes a formal specific diagnosis for this type of fructification; however, the characteristic appearance of the ostiolar collar due to the outward curvature of the cells of the ostiolar margin allows easy separation from the two preceding forms. Affinity with *Trichothyrina nigro-annulata* (Webster) Ellis, 1977 is suggested.

CONCLUSIONS

Previous records have concentrated upon Microthyriaceous forms within the Tertiary. The demonstration of Trichothyriaceous forms from the Upper Eocene is indicative that these fungi also were involved in the apparently rapid diversification of ascomycete groups during the Tertiary. Careful re-examination of material from pre-Tertiary deposits to establish the presence or absence of epiphyllous fungi, similar to the Trichothyriaceae would be of great interest. This might establish whether, with the advent of the angiosperms, the Trichothyriaceae arose as epiphyllous forms and only later attained their present far more specialized myco-parasitic nature.

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A NEW MULTIPLE-FLOATED *AZOLLA* FROM THE EOCENE OF BRITAIN WITH A BRIEF REVIEW OF THE GENUS

by M. E. COLLINSON

ABSTRACT. Megaspores and microspore massulae of *Azolla colwellensis* sp. nov. are described from the Upper Eocene, Upper Headon Beds of Colwell Bay, Isle of Wight. The megaspores possess a multifloated 'swim apparatus' with three tiers of floats. The floats are arranged in three groups of six. There is a distinct collar at the junction with the megaspore zone and hairs arising from this collar enmesh the floats. The microspore massulae possess occasionally septate, grapnel-tipped glochidia. This species is the youngest multifloated *Azolla* yet recorded and is the only multifloated species which possesses a collar. It further supports recent hypotheses that a number of lines of evolution have been involved in the development of extant *Azolla* species. A review of the sixty species recorded in the genus *Azolla* is presented in the form of a table showing stratigraphic ranges and features of the megaspores and massulae. Certain species are discussed in detail with relation to the morphology of *A. colwellensis*.

THE material here described was collected from folded strata of the Upper Headon Beds at the northern end of Colwell Bay, Isle of Wight (these beds are indicated on the section Pl. V in Keeping and Tawney 1881 and p. 103). The horizon sampled was 1·5 m from the cliff base at Linstone Chine (N.G.R. SZ 33058862), and comprised a purplish-black homogeneous silty clay.

Plant remains from the Upper Headon Beds in Colwell Bay have been described by Chandler (1963). Stratigraphically these beds have been considered either as Upper Eocene or Lower Oligocene in age. A discussion of this controversy may be found in Curry *et al* (1978). I follow these authors and Cooper (1976) in regarding these beds as Upper Eocene in age with the Eocene/Oligocene boundary at the base of the Bembridge Marls.

MATERIAL AND METHODS

The sample was disaggregated using hydrogen peroxide solution and separated into size fractions by sieving (Collinson 1978*a*, *b*). No faunal remains were recovered but the sample was rich in pyritic debris. Two macroplant species were present; the first a new species of a *Typha* seed (Collinson 1978*b*) and the second the *Azolla* which forms the subject of this paper. The sieved fractions were treated in hydrofluoric acid to remove unwanted mineral matrix. Specimens for SEM study were allowed to dry in air, mounted on stubs using durofix on a coverglass, and examined under Cambridge S 600, Mark IIA and S 180 scanning electron microscopes. Specimens studied with transmitted light were cleared using Schultze's solution for up to one hour and mounted in glycerine jelly. Transmitted and reflected light micrographs were taken using a Zeiss photomicroscope.

SYSTEMATIC DESCRIPTION

Family SALVINIACEAE Dumortier
Genus AZOLLA Lamarck
Section FLORSCHEUTZIA Kempf, 1968
(= KREMASTOSPORA Jain and Hall, 1969)
Azolla colwellensis sp. nov.

Plate 23, figs. 1–4, 7; Plate 24, figs. 1–9; text-fig. 1*a–e*

[Palaeontology, Vol. 23, Part 1, 1980, pp. 213–229, pls. 23–24.]

Syntypes. Plate 23, fig. 1 V59717a; Plate 23, fig. 7 V59718; Plate 24, fig. 7 V59717d; Plate 23, fig. 4 V59719. V numbers refer to catalogue numbers in the Palaeontology Department, British Museum (Natural History) London, where all the figured material has been deposited. Additional unfigured material has also been deposited, V59722.

Type locality. Linstone Chine (SZ 33058862) Colwell Bay, Isle of Wight, England.

Type horizon. Upper Headon Beds.

Diagnosis. Megaspore apparatus with eighteen (up to twenty-four) floats arranged in three tiers. Float zone of greater extent than megaspore zone and delimited by an apical cap and a basal collar at the junction with the megaspore. Total length 377–550 μm. Breadth (widest) 180–462 μm. Surface of floats sparsely hairy (suprafilosum *sensu* Fowler and Stennett-Willson, 1978), hairs originating from the collar. Exoperine columnar–rugulate obscured by infrafilosum derived from the rugulae. Endoperine granular pierced by small foveolae. Exine surface granular, total wall thickness 14–24 μm. Microspore massulae circular or elliptic (120×120–180×140 μm in diameter), attached to megaspores and also dispersed. Microspores at least eight per massula, trilete, subglobular–subcircular, 14–20 μm in diameter. Laesurae extending two-thirds of their radius. Glochidia with dilation and constriction below an anchor-shaped tip with recurved hooks. Occasional glochidia septate, with one or two distally placed septae.

Description. Megaspore apparatus with eighteen floats, closely packed and arranged in three tiers. Floats of the lower tier are often subdivided into two, one of which is very small, yielding a potential total of twenty-seven floats per megaspore although no more than twenty-four have been counted on the available material. The floats of the upper tiers are larger than those of the lower tier and they are quadrangular–hexagonal in surface shape (Pl. 23, figs. 1, 4). The float zone is larger than the megaspore zone (Pl. 23, fig. 7) and is delimited by a truncate apex with an apical cap (Pl. 23, figs. 1, 2; Pl. 24, fig. 2), and by a collar at the junction with the megaspore (Pl. 23, figs. 1, 4; Pl. 24, fig. 5).

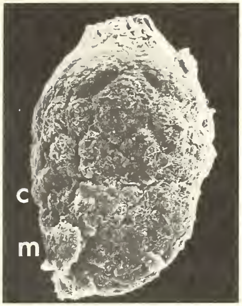
The eighteen floats are arranged in three groups of six (text-fig. 1*d*), each group with one large upper, two smaller middle, and three smallest lower floats (fifteen specimens were available in which the exact number and arrangement of floats was clearly visible). The syntype V59719 (Pl. 23, fig. 4*a*–*d*), shows this arrangement but also reveals the erroneous impression which can be gained by certain views of the specimen. When compression has obscured all but two flattened faces (e.g. the apparent view of Pl. 23, fig. 4*c*), it appears that there are only twelve to fourteen floats per specimen, six to seven on each flattened face. Alternatively as in Plate 23, fig. 2 and Plate 23, fig. 4*a* there may appear to be only four floats per flattened face.

The collar is visible externally below the lowest tier of floats (Pl. 23, figs. 1, 4) and is partly composed of intertwined hairs (suprafilosum) (Pl. 24, fig. 5), which are continued into the central region of the float zone (text-fig. 1*a*) and on to the surface of the floats (Pl. 24, fig. 5 *left*) thus enmeshing them. On the collar, the suprafilosum originating in the collar and the infrafilosum originating from the megaspore exoperine, are intertwined.

EXPLANATION OF PLATE 23

Figs. 1–4, 7. *Azolla colwellensis* sp. nov. Upper Headon beds, Colwell Bay, Isle of Wight. 1, megaspore, syntype, V59717a, showing external appearance of the three tiers of floats, the basal collar (c) and an attached massula (m), SEM, × 130. 2, megaspore, V59720, showing less well-defined view of floats, comparable with that in fig. 4*a*. Note also hairy exoperine and truncate apical cap, SEM, × 130. 3, razor-cut vertical section through a megaspore V59717b. Five floats have been sectioned, two on the right, three on the left. The pseudovacuolate collar appears at the base of the float zone and the hairy central column is visible. Damage in the megaspore wall is due to pyrite crystals, SEM, × 130. 4*a*–*d*, megaspore, syntype, V59719, showing the float system as viewed in reflected light, rotated through a series of 90° angles. Note the sharp junction between two groups of six floats in 4*a*, and the irregular boundary in 4*c* (right edge). The collar (c) also stands out, being of similar texture to the floats, RLM, × 125. 7, megaspore, syntype, V59718, showing the proportions of the megaspore and float zone, TLM, × 100.

Figs. 5, 6. *A. schopfii* Dijkstra, Palaeocene, Slim Buttes, Texas. 5, megaspore showing trilete mark, oval shape, and large foveolae in megaspore wall unobscured by hairs, TLM, × 100. 6, another megaspore showing the loose arrangement of the floats and the rounded shape, TLM, × 100.



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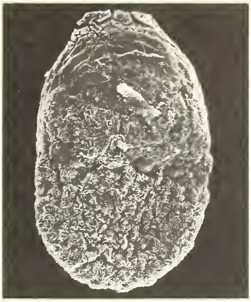

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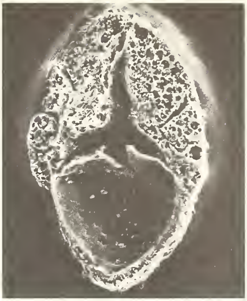

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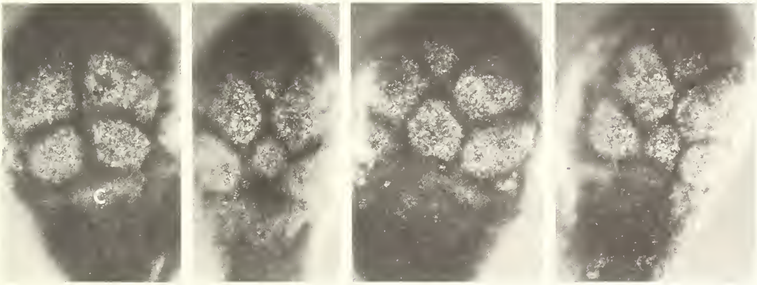

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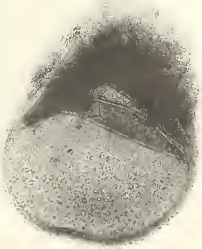

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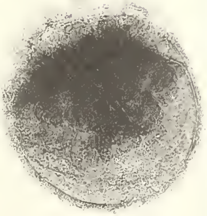

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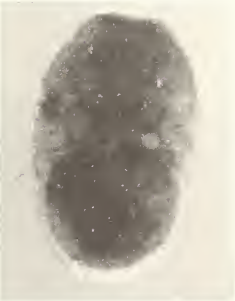

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COLLINSON, *Azolla*

The floats themselves are distinctly pseudovacuolate structures which extend inwards to the hairy central region (Pl. 23, fig. 3; Pl. 24, fig. 1; text-fig. 1*a*). These hairs extend in an umbrella-like expansion over the surface of the floats thus enmeshing them and acting as a retention mechanism.

Total length of megaspore apparatus 377–550 μm (mean 437 μm), breadth 180–462 μm (mean 325 μm). Length of float zone 200–350 μm, length of megaspore zone 125–240 μm (fifty specimens measured). Upper part of megaspore partly covered by the collar and lower tier of floats, trilete mark not visible. The megaspore is densely hairy externally (Pl. 24, fig. 4) and the perine is divisible into two zones when seen in sectional view. The exoperine is columnar–rugulate and obscured in surface view by intertwined hairs (infrafilosum) arising from the tips of these rugulae (Pl. 24, fig. 3; text-fig. 1*b*). The endoperine is granular, pierced by small foveolae, variable in thickness, and with foveolae extending to form the pseudovacuolate part of the collar (Pl. 24, fig. 6). Exine surface also granular, exine 3–5 μm thick. Total megaspore wall thickness from 14–24 μm.

Microspore massulae (Pl. 24, fig. 7) circular or elliptic, frequently aggregated in groups of four or eight. Eight megaspores seen with massulae attached. Number of microspores greater than eight but not clearly discernible. Microspores trilete, subtriangular–subglobular (Pl. 24, fig. 8; text-fig. 1*c*). Glochidia (Pl. 24, fig. 9; text-fig. 1*e*) 40–50 μm in length, of almost equal width throughout their length but with a prominent dilation and constriction immediately below the tip. Tip anchor shaped with recurved hooks (Pl. 24, fig. 9). Occasional glochidia septate with one or two distal septae (Pl. 24, fig. 8; text-fig. 1*e*). A single massula may possess both septate and non-septate glochidia.

FEATURES OF SYSTEMATIC SIGNIFICANCE

Float number and arrangement

The systematics of *Azolla* species has been characteristically based on the number of floats in the megaspore apparatus. Three, nine, or more (fifteen to twenty-four) represent the three main categories (Hall 1969*a*). Snead (1969) remarked upon the problem of floats not always being easily distinguishable, and advocated, as did Kempf (1969*b*), the use of megaspore wall and perispore structure in systematic studies. Snead had, however, attempted to study and illustrate all of his species by transmitted light microscopy. Hall and Swanson (1968) showed how in *A. montana* Hall and Swanson emend. Jain and Hall, 1969 the individual floats are indistinguishable in transmitted light, as they are in *A. colwellensis* (Pl. 23, fig. 7). They can be well displayed using reflected light with a dark background (Pl. 23, fig. 4).

Table 1 lists all the known *Azolla* species and shows that many possess numerous floats in the megaspore apparatus. A number of these are categorized as N or (N). These have numerous floats

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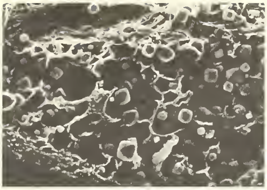
EXPLANATION OF PLATE 24

Figs. 1–9. *Azolla colwellensis* sp. nov., Upper Headon Beds, Colwell Bay, Isle of Wight. 1, detail of section in Plate 23, fig. 3 showing pseudovacuolate nature of the floats and hairy central column (upper edge of figure). Note the abundance of pyrite crystals, SEM, × 500. 2, detail of the apical cap from Plate 23, fig. 1, SEM, × 150. 3, detail of the megaspore wall, V59717c, showing the exine (e), endoperine (en), and exoperine (ex); cf. text-fig. 1*b*, SEM, × 1750. 4, detail of the hairy surface of the megaspore in Plate 23, fig. 1, SEM, × 500. 5, detail of the collar surface with float zone to left, from Plate 23, fig. 1, SEM, × 500. 6, detail of section through the collar zone at the junction between the collar (left) and megaspore (right). Note the merging of the supra and infra filosal hairs, and the extension of the endoperine to form the pseudovacuolate collar, SEM, × 1000. 7, a single massula from a cluster, syntype, V59717d, SEM, × 800. 8, detail of a fragment of a massula, V59721, showing a trilete microspore (m) and septate glochidia with anchor-shaped tips, TLM, × 1000. 9, detail of the tip of a glochidium, SEM, × 3500.

Figs. 10–12. *A. prisca* Reid and Chandler emend. Fowler, 1975. 10, specimen of typical form from the Bembridge Marls, Hamstead Ledge, Isle of Wight, V60110. Note three floats and massulae aggregated around the collar, SEM, × 125. 11, specimen from the Lower Headon Beds (Unio Band) of Hordle, Hampshire, V60111, a new record for this species, SEM, × 125. 12, an atypical specimen from the Bembridge Marls of Hamstead Ledge showing septation of the lower tier of floats, V60112, SEM, × 125.



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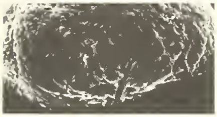

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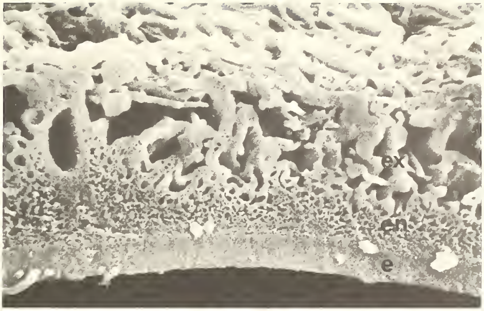

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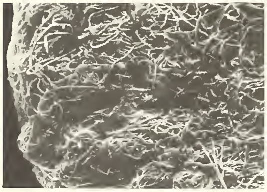

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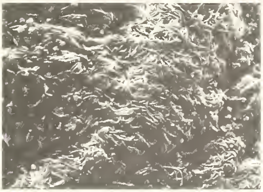

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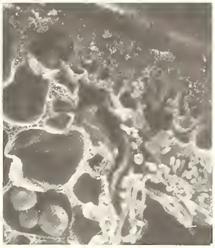

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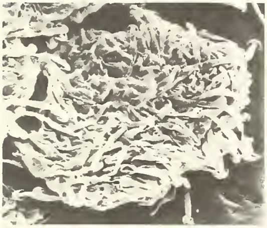

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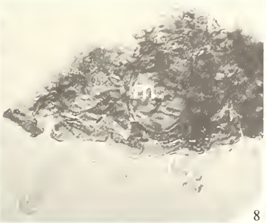

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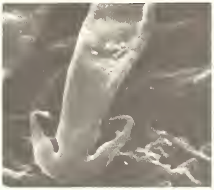

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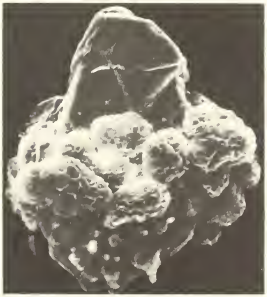

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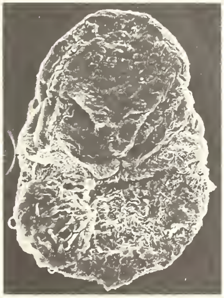

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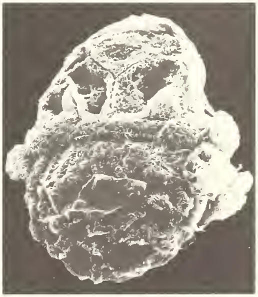

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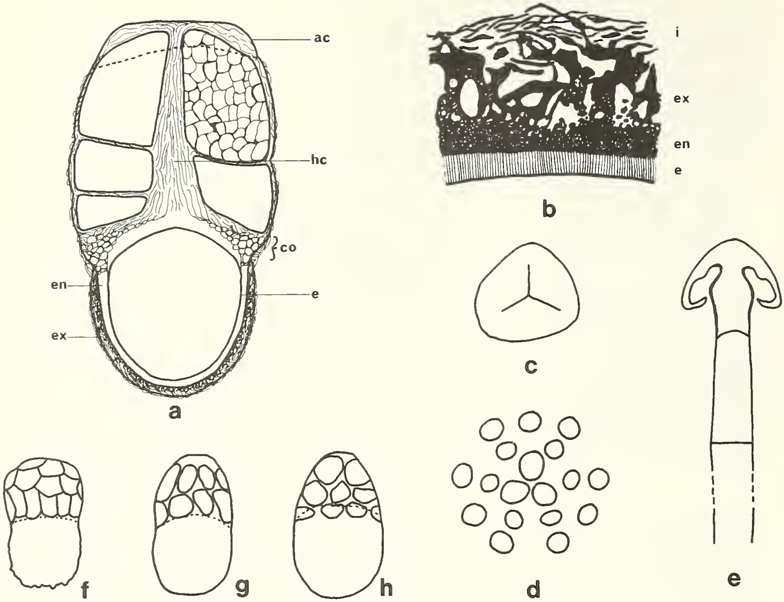
COLLINSON, *Azolla*



TEXT-FIG. 1*a–e*. Features of *Azolla colwellensis* sp. nov., Upper Headon Beds, Colwell Bay, Isle of Wight. *a*, longitudinal section of the megaspore apparatus, × 150. *b*, section showing the megaspore wall stratification, × 1000. *c*, microspore, × 1000. *d*, diagrammatic, expanded apical view of the float distribution. *e*, detail of the grapnel tip of a glochidium, × 3000. *f–h*. Diagrams showing the float arrangement in three species of *Azolla* based on the literature summarized in Table 1, × 50. *f*, *A. teschiana*, *g*, *A. montana*, *h*, *A. anglica*. ac = apical cap; hc = hairy central region (suprafilosum); co = collar; e = exine; en = endoperine; ex = exoperine; i = infrafilosum.

which are indistinguishable either in actual number or in morphology, and for which no new reflected light observations are available. Those species described by Snead (1969) have already been mentioned, but in other species, e.g. *A. elegans* Jain and Hall, the floats have been lost during preservation and the preservation state itself may often obscure the float number due to compression etc. A number of other species of *Azolla* possess a large number of floats, but these are recognizable and countable entities, e.g. *A. schopfii* Dijkstra (Pl. 23, figs. 5, 6), where fifteen to twenty-two floats have been recognized. They are attached to the megaspore by a weft of hairs arising in the central region. Floats enmeshed in this way are often obscured when viewed by SEM (e.g. *A. velus* in Martin 1976*a*). Using transmitted light, however, it is clear that the floats, although recognizable structures, are held together only loosely, being easily dislodged (Pl. 23, figs. 5, 6). Reflected light micrographs (Sweet and Chandrasekharam 1973), do reveal the floats clearly for *A. schopfii* and indicate the variability in their arrangement as suggested by transmitted light observation. This somewhat loose arrangement of the floats is further expressed in the range of morphology of the megaspore and the float zone. *A. velus* and *A. stanleyi* (see Table 1) have a similar loose aggregation of floats.

A. colwellensis, however, viewed also in transmitted light for direct comparison (Pl. 23, fig. 7), has a much more compact float zone and a consequent uniformity of megaspore and float zone shape (see Pl. 23). Other species with a similar compact arrangement of many but countable floats as recorded in the literature, are summarized in Table 1 and include *A. teschiana* Flörshutz, *A. montana* (Hall and Swanson), *A. anglica* Martin, *A. bulbosa* Snead, and *A. distincta* Snead.

A. teschiana figured by Snead (1969) does not reveal any float pattern. Dijkstra (1961) figured a reconstruction from Flörschutz (1945) which has been vindicated by SEM observations (Martin 1976*a*). There are twenty-four floats of very similar sizes arranged in three tiers in a closely compact mass (text-fig. 1*f*). *A. bulbosa* appears to be very similar to *A. teschiana* from Snead's figure and description. *A. distincta* when studied by SEM (Hall 1974) revealed two tiers of floats, the upper tier larger than the lower. The floats in *A. montana* were originally described as surface features only, barely differentiated from the dome-shaped columella, but Martin (1976*a*) states in a footnote that Hall has suggested that there may be a well-defined central column in this species. If this is the case, then *A. montana* may be quite similar to *A. colwellensis*. However, Hall's (1974) SEM illustration demonstrates, as noted by Hall and Swanson (1968) and Jain and Hall (1969), that *A. montana* has only two tiers of floats, all being of similar size and not apparently arranged in three groups of six (see text-fig. 1*g*). In addition, the float zone is equal to, or less than, the megaspore zone in extent. *A. montana* and *A. colwellensis* are thus distinct species in this respect. *A. anglica* is most similar to *A. colwellensis* in its float zone arrangement, having up to twenty-four floats in three tiers (text-fig. 1*h*). The float zone, however, only occupies one-third of the entire megaspore apparatus.

Whilst it is necessary to re-examine all species previously seen only with transmitted light, before a complete assessment of multifloated *Azolla* species can be made, *A. colwellensis* appears to be distinct in its float pattern from all other recorded species. It is, however, most similar to *A. montana* and *A. anglica*.

Retention of floats, and presence of cap and collar

Two methods of float retention have been described for *Azolla* species. The first is the development of hooked maniculae from the central column (Martin 1976*a*), as for example in *A. anglica*, *A. velus*, and *A. teschiana*. These maniculae supposedly entangle with hairs on the floats, and Martin suggests that they will occur in all species of Section Kremastospora. They have not been recorded by other workers and do not occur on *A. colwellensis*.

The second method is the trapping of the floats within a domed meshwork of hairs (suprafilosum) derived from a basal collar as in *A. prisca* (Fowler, 1975). In less differentiated species, a weft of hairs arises from the proximal megaspore surface and similarly enmeshes the floats, as in *A. schopfii*, but no distinct basal collar is present. The float system is thus very variable in appearance, the floats being securely attached to the megaspore, but able to shift in position with respect to it. The term loose float arrangement has been used here to describe this morphology. A very similar condition exists in Cretaceous genera similar to *Azolla*, e.g. *Azollopsis* and *Glomerisporites* (Hall, 1974).

Martin (1976*a*) emphasized the importance of the retention mechanism and commented that the collar occurred relatively late; in Upper Oligocene and younger species. However, Sahni (1941) recorded *A. intertrappea* (with a 'reflexed flange' possibly a collar) in the Eocene, and I here record *A. prisca* from the Eocene (Pl. 24, fig. 11), which has a very well-defined collar. Thus the collar occurs in Eocene nine- and three-floated species, and is here recorded for the first time in an Eocene multifloated species, namely *A. colwellensis*.

The existence of an apical cap has been recorded in two multifloated species—*A. montana* and *A. anglica*—but not in conjunction with a collar as in *A. colwellensis*. Martin (1976*a*) considered that the cap (apical membrane) along with the basal collar, constituted the retention mechanism, and felt that the hairy weft was useful in retention only in conjunction with hooked maniculae. The cap, however, as part of the original megasporangial wall, may be present in all *Azolla* species; its absence being due to lack of preservation. Clearly the dome-shaped suprafilosum passing up through the centre of the float zone and out over the apex, would act as a float retention mechanism without an apical cap. Although the cap is usually preserved on species with a basal collar, this is probably because the float zone is compact rather than because the cap is causing the compact arrangement (on *A. teschiana* for example the cap is absent). Prior to the development of a distinct collar, a diminutive collar—merely an extension of the perine—would assist in float retention, and produce a compact float arrangement. This may occur, for example, on *A. anglica* where it is noted that the distinction between the zones of the perine is lost at the megaspore apex. The fact that many specimens of *A. anglica* had lost their floats, suggests that this or the possible maniculae, were not very effective float retention mechanisms. It is the occurrence of the collar, and the associated development of a central zone within the float zone through which the suprafilosum (derived from the collar) extends up to and over the apex, which is most important in float retention. It is possible that on some species, maniculae also aided float retention, but in my opinion their presence is of little significance when compared with the above mechanism.

It has been recognized that nine- and three-floated species (with compact float arrangements) are triseptate, with the float zone divided into three compartments formed from the suprafilosum. In multifloated *A. colwellensis*, no triseptation has been observed, but the floats have been seen to occur in three distinct groups. The junction between the groups is sometimes sharp (Pl. 23, fig. 4*a*), and is thus very similar to the septum, as for example, in *A. prisca*. In other places, however, there is no vertical boundary between two groups of floats (Pl. 23, fig. 4*c* right hand edge). It does appear that, along with the development of a collar and dome-shaped suprafilosum, came a tendency towards the triseptate condition, which is so far only known to be fully developed in nine- and three-floated species.

A. colwellensis is the youngest recorded multifloated *Azolla* species, and is the only multifloated species with a distinct collar aiding float retention. In addition, it has a well-developed dome-shaped suprafilosum, originating from the collar, and passing upwards through the centre of the float zone, showing an arrangement of the floats in three groups with a tendency towards triseptation.

Megaspore wall structure

Snead (1969) and Kempf (1969*b*) have both emphasized the importance of megaspore wall structure in the classification of *Azolla* species. This feature however is not usually referred to in the diagnoses of the various sections within the genus (see Fowler 1975 and Hall and Swanson 1968), which are based on the features discussed above, and on the microspore massulae (see below). Nevertheless, the literature on detailed sporoderm architecture is increasing; Fowler and Stennett-Willson (1978) and Martin (1976*a*) have described Recent species, and Martin (1976*a*), Friis (1977), Fowler (1975), Martin (1976*b*), and Snead (1969) have provided detailed description and illustration of fossil forms. Earlier literature is, however, poorly illustrated, and there is considerable difficulty in comparing the many known species. Confusion exists particularly between surface and sectional based descriptions.

A three-layered sporoderm structure is characteristic of *Azolla* species comprising the exine (megaspore wall proper), the endoperine, and the exoperine. In some fossil species the detail of the surface of the megaspore exoperine is entirely obscured by a covering of hairs which are derived from the exoperine itself, forming the infrafilosum, as in *A. colwellensis* (Pl. 23, fig. 2; Pl. 24, fig. 4). *A. prisca* also possesses a hairy exoperine, but in this case the hairs are derived from particular areas (the tubercles—Pl. 24, fig. 10), and do not totally obscure the megaspore surface.

In other fossil species, for example, *A. velus* (see Martin 1976*a*), a hairy covering extends only part way down the megaspore, and thins out completely at the distal face. These hairs are derived from the collar region, and are in fact part of the suprafilosum, not part of an exoperinal infrafilosum. In these species the exoperine is usually visible in surface view and is variously foveolate, reticulate, rugulate, or tubercled (see *A. schopfii*, Pl. 23, figs. 5, 6). Such species include *A. teschiana* and *A. anglica* (Martin, 1976*b*), *A. nikitinii* (Friis, 1977), *A. ventricosa* (Friis, 1977), *A. montana* (Jain and Hall, 1969), and *A. schopfii* (Sweet and Chandrasekharam, 1973). In *A. montana* the outermost hairy zone, termed the perispore (Hall and Swanson 1968), is very easily detached and is clearly not derived from the underlying exoperinal wall elements. The wall sculptural elements are usually clavate in sectional view and variously united along their length or at their tips, to produce the effect of a surface reticulum. In some of this group of species the hairs only extend a very short distance below the float zone, as in *A. bulbosa* and *A. barbata* (Snead, 1969).

Difficulties arise when considering a number of other species where the descriptions do not make clear whether the hairy outer layer of the megaspore is in fact derived from the collar (is suprafilosum), or derived from the exoperine (is infrafilosum). In the latter case it will not be detachable. Multifloated species where such information is lacking, include *A. distincta*, *A. filosa*, *A. lauta*, *A. pilata*, *A. fistulosa*, and *A. conspicua* of Snead (1969), and *A. fragilis*, *A. elegans*, and *A. stanleyi* of Jain and Hall (1969). Of these species *A. fragilis* (together with *A. extincta* of Jain 1971) is considered synonymous with *A. schopfii* (Sweet and Chandrasekharam, 1973). *A. fistulosa* is considered by Jain (1971) to be synonymous with *A. distincta*, and is shown to have 'an often lost' (i.e. detachable) hairy layer, derived from the suprafilosum. *A. pilata* was transferred to *Salvinia* by Jain (1971).

The thickness of the wall, ranging from 26 to 145 μm in the remaining multifloated species where the origin of the hairy layer is uncertain, prevents their being closely comparable with *A. colwellensis*. None of the previously figured sections of sporoderm is exactly comparable with that of *A. colwellensis*; the elements of the inner zone of the exoperine are usually predominantly clavate beyond a thin columnar zone (Fowler 1975, text-fig. 1C; Martin 1976*b*, text-fig. 1*a*). *A. colwellensis*, however, has no defined columnar zone, and has coalescing rugulae rather than a clavate structure (Pl. 24, fig. 3; text-fig. 1*b*).

Although it has not been possible to make a fully detailed comparison, it seems clear that the sporoderm of *A. colwellensis* is distinct from that of all other fossil species with a similar megaspore apparatus. In the possession of the exoperinal hairs, the species is similar to *A. prisca*, but otherwise the two species are very different. Those species with the most similar float arrangement—*A. anglica*, *A. montana*, and *A. schopfii*—do not possess hairs arising from the exoperine.

Microspore massulae

Features of the microspore massulae of *Azolla* species are summarized in Table 1. Anchor-shaped glochidia with a distal dilation (gad on Table 1) occur throughout the range of the genus on both multi-, nine- and three-floated forms. They occur on species with a single columellate float, for example in *A. simplex* and *A. primaeva*, on three-floated *A. indica* and *A. intertrappea*, on nine-floated *A. prisca*, and on multifloated *A. montana* and *A. anglica* (which are considered most similar to *A. colwellensis* in float arrangement), all in pre-Oligocene strata. Their occurrence is probably related to the possession of hairs on the megaspore surface, to which the anchor-shaped tips can become attached or enmeshed. Whether these hairs are derived from the suprafilosum, and occur around the collar only, or are derived from the exoperine (infrafilosum) and occur all over the megaspore, may be of very little significance for massula attachment. It is possible that the possession of a hairy protruding collar (an area where hairs of both types may become intertwined), results in the attachment of many massulae in that area, nearest to the proximal megaspore face, as is often the case in *A. prisca* (Pl. 24, fig. 10).

Anchor-shaped glochidia with a distal dilation which are also septate, occur only in *A. colwellensis* and *A. anglica* among multifloated species. They also occur in the Eocene *A. intertrappea* and in two modern species. Godfrey *et al.* (1961) recorded both septate and non-septate glochidia on the same massula in *A. caroliniana*. It is therefore probably unwise to assign any particular significance to the presence of septae. Also, as Fowler (1975) suggests, the junction between the solid head of the glochidium and the hollow stalk may in some cases have been misinterpreted as a septum.

TABLE 1.

Species	References	Veg.	Megaspores	Massulae	Age
Azolla simplex	Hall 1969*b*		Ic	gad	Lower Cretaceous
A. barbata	Snead 1969 Hall and Bergad 1971 Hall 1974		(N) ii	+gch	Cretaceous–Palaeocene
A. extincta	Jain 1971 (= *A. schopfii*, see Sweet and Chandrasekharam 1973)		(N)	+eg	Cretaceous
A. geneseana	Hills and Weiner 1965 Hall and Swanson 1968 Srivastava 1968		3/1c	ga	Cretaceous
A. cretacea	Stanley 1965 Srivastava 1968 Hall 1974 Srivastava 1975		?as *A. montana* Jain and Hall, 1969 or unknown	gad	*?Cretaceous, Palaeocene, and Lower Eocene
A. circinata	Oltz and Hall in Hall 1968			gch	Cretaceous
A. gigantea	Bergad and Hall 1971			gad	Cretaceous
A. sagittifera	Srivastava 1968			gab	Cretaceous
A. hamata	Srivastava 1968			gch	Cretaceous
A. pilata	Snead 1969 (transferred to *Salvinia* in Jain 1971)		floats lost		Cretaceous
A. conspicua	Snead 1969		(N)		Cretaceous
A. lauta	Snead 1969		(N)		Cretaceous and Palaeocene
A. fistulosa	Snead 1969 (= *A. distincta* Jain, 1971)		(N)		Cretaceous and Palaeocene
A. filosa	Snead 1969		(N)		Cretaceous and Palaeocene
A. distincta	Snead 1969 Hall and Bergad 1971 Hall 1974 Jain 1971		N: ?15 ii/iii	+ga	Cretaceous and Palaeocene
A. schopfii	Dijkstra 1961 Snead 1969	veg	15–18 ii/iii	ga	Cretaceous and Palaeocene
	Sweet and Chandrasekharam 1973		15–22 iii	gch/simple	
A. montana	Hall and Swanson 1968 emend. Jain and Hall 1969 Hall 1974		10/15–20 ii	+gad	Cretaceous, Palaeocene, and Lower Eocene
A. bulbosa	Snead 1969		18 iii		Palaeocene
A. fragilis	Jain and Hall 1969 (= *A. schopfii* Sweet and Chandrasekharam 1973)		(N)		Palaeocene
A. elegans	Jain and Hall 1969		floats lost		Palaeocene
A. stanleyi	Jain and Hall 1969		15–N	+ga	Palaeocene
A. velus	Dijkstra 1961 Jain and Hall 1969 nov. comb. Martin 1976*a*		10–N ii	+ga	Palaeocene
A. teschiana	Flörschutz 1945 Dijkstra 1961 Martin 1976*a*		24 iii	+ga	Palaeocene
A. anglica	Martin 1976*b*		up to 24 iii	? +gads	Palaeocene
A. berryi	Brown 1934	veg			Middle Eocene

TABLE 1 (*cont.*)

Species	References	Veg.	Megaspores	Massulae	Age
A. intertrappea	Sahni and Rao 1943 (Sahni 1941) Hall 1969*a* Trivedi and Verma 1971	veg	3	+gad	Eocene
A. indica	Trivedi and Verma 1971		3	gads	Lower Eocene
A. primaeva	Arnold 1955 Hills and Weiner 1965 Hills and Gopal 1967 Hall 1969*a*	veg	Ic	gad	Eocene
A. antiqua	Dorofeev 1959*a*		t 6–9 ii		Upper Eocene–Lower Oligocene
A. colwellensis	This work		18(–24) iii	+gads	Upper Eocene
A. prisca	Reid and Chandler 1926 emend. Fowler 1975 This work	veg	t 9 ii	+gad	Upper Eocene–Lower Oligocene
A. suchorukovii	Dorofeev 1968*b*		t 9 ii		Oligocene
A. nana	Dorofeev 1959*a*		t 9 ii	eg	Oligocene
A. turgaica	Dorofeev 1959*a*		t 9 ii	eg	Oligocene
A. sibirica	Dorofeev 1959*a*, 1962, 1963		t 9 ii		Middle Oligocene
A. parapinnata	Dorofeev 1962, 1963		t 9 ii		Oligocene
A. ventricosa	Nikitin 1948 Dorofeev 1959*a*, *b*, 1962, 1963 Nikitin 1965 Friis 1977 (First formal diagnosis in Dorofeev 1959*b*)		t 9 ii	eg	Oligocene–Miocene
A. vera	Kryshtofovitsh 1952	veg			Oligocene
A. bohemica	Pacltova 1958			gad	Upper Oligocene–Lower Miocene
A. nikitinii	Dorofeev 1955*a*, *b*, 1959*b* Lancucka-Srodoniowa 1958 Dorofeev 1962, 1963 Friis 1977		t 9–12 ii		Upper Oligocene and Miocene
A. tertiara	Berry 1927	veg			? Miocene/Pliocene
A. tuganensis	Dorofeev 1962, 1963 Friis 1977		t 3 i	+ga	Upper Oligocene and Miocene
A. glabra	Nikitin cited in Dorofeev 1955*a*, *c*, 1959*b* Lancucka-Srodoniowa 1958		3 i	gas	Upper Oligocene and Miocene
A. tomentosa	Nikitin 1948 Dorofeev 1959*b*, 1962, 1963 Bertelsen 1974		3 i	+gas	Upper Oligocene and Miocene
A. aspera	Dorofeev 1963		t 9–12 ii	+eg	Upper Oligocene and Miocene
A. sulaensis	Dorofeev 1968*a*		t 9 ii		Middle Miocene
A. parvula	Dorofeev 1968*a*		t 9 ii		Upper Miocene
A. pulchella	Dorofeev 1969		t 9 ii		Upper Miocene
A. ucrainica	Dorofeev 1968*a*		3 i	ga	Upper Miocene
A. roemoensis	Bertelsen 1974		t 9 ii		? Upper Miocene
A. pseudopinnata	Nikitin 1957 Lancucka-Srodoniowa 1958 Dorofeev 1959*a*, *b*, 1963		t 9 ii		Upper Miocene–Lower Pliocene
A. pyrenaica	Flörschutz and Amor 1960 Potonié 1962		3 i	ga	Upper Pliocene and Pleistocene

TABLE 1 (*cont.*)

Species	References	Veg.	Megaspores	Massulae	Age
A. tegeliensis	Flörschutz 1938 emend. Bertelsen 1972 Potonié 1962 Kempf 1969*a*		t 9 ii	? *A. danica*	Upper Miocene, Pliocene and Pleistocene
A. danica	Bertelsen 1972			g simple, hair-like, bifurcating occasionally	Lower Pleistocene
A. interglacialica	†Nikitin 1957 Dorofeev 1956 Kolesnikova 1964		3 i	+gads	Pliocene and Pleistocene
A. filiculoides Lam.	Madler 1954 Godwin 1975 Martin 1976*a* Fowler and Stennett-Willson 1978 Pieterse *et al.* 1977	veg	3 i	+gads	Upper Pleistocene and Recent
A. microphylla Kaulfuss	Svenson 1944 Fowler and Stennett-Willson 1978	veg	3 i	+gs	Recent
A. caroliniana Willd.	Strauss 1952 ‡Martin 1976*a* Svenson 1944 Godfrey *et al.* 1961 Pieterse *et al.* 1977	veg	3 i	+gads	Upper Pleistocene and Recent
A. mexicana Presl.	Svenson 1944	veg	3 i	+gs	Recent
A. nilotica Decaisne	Martin 1976*a* Fowler and Stennett-Willson 1978	veg	9 ii	+eg	Recent
A. pinnata R. Brown including *A. imbricata* (Roxburgh) Nakai	Sweet and Hills 1971 Martin 1976*a* Fowler and Stennett-Willson 1978	veg	9 ii	+g straight unhooked	Recent

* *Azolla cretacea* is extended into the Eocene if accepted as belonging to *A. montana*. Jain and Hall (1969), however, suggested the retention of the separate name *A. cretacea* for isolated massulae of this type.

† *A. interglacialica* Nikitin, 1957 is considered by Lancucka-Srodoniowa (1958) to be identical with *A. filiculoides*.

‡ Keith Fowler (pers. comm. 1978) believes that Martin (1976*a*) examined megaspores of *A. microphylla* in mistake for *A. caroliniana*.

Explanation to the abbreviations:

Veg.: Indicates that vegetative material is known.

References: The first reference indicates the author of a fossil species.

Megaspores: Number of floats: () = indistinct; N = Numerous. Float characters: t = triseptate; c = columellate. Float numbers: Arabic figures. Number of float tiers: Roman figures.

Massulae: + = massula recorded attached to megaspore; eg = eglochidiate; ga = glochidia anchor-shaped; gad = glochidia anchor-shaped with a distal dilation; ch = glochidia coiled and hair-like; b = barbed; s = septate.

DISCUSSION AND PHYLOGENETIC IMPLICATIONS

The previous section has demonstrated the differences between *A. colwellensis* and those species which are of a similar morphology, or occur at a close stratigraphic horizon. The data are summarized in Table 1 where it may be seen that a similar combination of features occurs only in *A. anglica* and *A. montana*. In the latter the floats are shown to be usually in two tiers (Hall 1974), their number being very irregular; the float zone occupying less than half, usually one-third, of the megaspore apparatus, and the float arrangement, although compact, is very variable, as is the megaspore apparatus shape. The glochidia are shorter than those of *A. colwellensis* and are non-septate. *A. anglica* has a float zone very similar in float number and arrangement to that of *A. colwellensis*; however, the float zone usually occupies only about one-third of the megaspore apparatus. The glochidia are shorter and are very narrow for half their length, expanding to a broader end with a weak distal dilation. Neither *A. montana* nor *A. anglica* possesses a hairy perispore arising from the exoperine, or a collar delimiting the base of the float zone.

The existence of *A. colwellensis* as a distinct species of *Azolla* is therefore established. It is similar to the species mentioned above and also to *A. schopfii*, *A. teschiana*, *A. velus*, and *A. distincta*. Of these, *A. velus* and some specimens of *A. distincta*, have floats in two tiers, the upper larger than the lower, whilst the other species have floats in three tiers. In *A. teschiana* (text-fig. 1*f*), all the floats are of a similar size, and so it may be suggested that this species represents the least differentiated multifloated form.

It has been demonstrated by Martin (1976*a*) that the floats of *Azolla* are derived from aborted megaspores. His summary of the life cycle shows that thirty-two potential megaspores are produced and thirty-one abort. He has also demonstrated the presence of immature megaspores in the perine of the mature megaspore, and also in the pseudovacuolate floats. He suggested that if twenty-four floats are the result of extension of the tissue of twenty-four aborted megaspores, then a further seven aborted megaspores must be embedded in the tissue of the mature megaspore perine, though these actual figures have yet to be proven. Such a hypothesis separates the megaspores into four sets of eight, with three sets forming the floats. Twenty-four floats, one per aborted megaspore, would thus be the maximum, and it is interesting to note that not more than twenty-four floats (but up to twenty-four in three cases) have been recorded. Further, it seems likely that the so-called septation of floats into a smaller one and a larger one is merely the reduction in size of one float, prior to a condition where it will have merged with the larger float. However, the record of triseptation of all of the twenty-four floats in *A. teschiana* (Hills and Gopal, 1967, p. 1088) is not in harmony with this view. Nevertheless, it seems plausible to accept twenty-four as the basic float number in *Azolla* species. By the merging of various floats it is possible to derive any of the smaller numbers from this figure.

The occurrence of the floats in two or three tiers need not be of any particular phylogenetic significance, as even in those species with a compact float arrangement, the positioning of the floats will be partly controlled by the space available in the float zone. Also, the upper tier of floats will by this reasoning tend to be larger than the lower tier. The upper tiers may well contain a higher number of aborted megaspores.

The presence of three- and one-floated forms in the same stratigraphic levels as the many-floated forms, shows that it is not certain that they are derived from the latter by reduction in float number. It has, however, been suggested (Jain 1971) that all these early three- and one-floated species (see Table 1) may need reinterpretation, due to lack of previous detailed study, and difficulties in observation of certain preservation states. Accepting their existence, however, indicates that all the abortive megaspores became aggregated into one or three groups in some species, at an early stage in the evolution of the genus. These species would probably then represent a different lineage from the multifloated species, and it is possible that four lineages may be recognized with one, three, nine, and more than nine floats, as suggested by Hall (1969) and Martin (1976*a*).

Previous authors have attributed considerable significance to the fifteen floats of *A. schopfii*, but this has now been shown to have up to twenty-two floats (Sweet and Chandrasekharam 1973). It is very important in future studies of multifloated *Azolla*, that the basic float number should be recognized, for example eighteen in *A. colwellensis*. All the multifloated species except *A. teschiana*, may have a basic number of eighteen, but in *A. anglica* it could be twenty-four, and in *A. montana*, *A. distincta*, *A. stanleyi*, *A. schopfii*, and *A. anglica* it could be fifteen. In more recent species, distinct records of nine- and three-floated forms occur, but still examples of six and twelve floats are known. Thus a series of 24, 18, 15, 12, 9, 6, 3, 1, floats is known, which lacks only one unit (twenty-one floats which could easily be the number for one of the species not well studied), to include all the permutations of the successive merging of one further abortive megaspore, in each part of the three-partite float zone. Similarly, the most reliable records 24, 18, 9, and 3, represent the merging of two abortive megaspores in each part of the float zone.

The variation in float number in *Azolla* species could therefore be due to the variation in the grouping of twenty-four of the abortive megaspores within the float zone. Species occur with one abortive megaspore per float, each float being of similar size. Other species, for example those with eighteen floats, have the upper tier of floats larger, perhaps each containing three abortive megaspores, with one each in the lower floats. Three-floated forms may have eight abortive megaspores to each float. That these morphologies have arisen in any particular sequence is not substantiated by the fossil record, which actually indicates that there may have been a number of separate lineages, species from each existing contemporaneously.

That the merging of the abortive megaspores into groups within the floats is a very 'plastic' feature is substantiated by the range of float numbers recorded for some species (Table 1). During this study, one specimen of *A. prisca* (Pl. 24, fig. 12), collected from the Bembridge Marls, was found to have two floats at the positions of each float in the lower tier, giving a total of fifteen floats.

Apart from the attempt to elucidate *Azolla* phylogeny in terms of variation of float numbers, variation in glochidia morphology has also been used. Mahabale (1963) suggested that a reduction had occurred in glochidia form, assuming that septate glochidia with anchor-shaped tips were primitive and reduced through three stages: the first non-septate with anchor-shaped tips; the second not anchor-shaped, merely hair-like; and the third missing altogether. Jain (1971) objected to this hypothesis on the basis that all these features could be found in Cretaceous *Azolla* and related genera. The data on Table 1 support this claim, and show that there is no distinct change of trend in glochidia morphology supported by the fossil record. The glochidia morphology is to some extent adapted to the megaspore structure; those with anchor-shaped tips being ideal for trapping on the hairy megaspore surface. However, this hairy surface may be derived from the megaspore exoperine or from the collar region, so it does not necessarily indicate a close phylogenetic relationship for all species with anchor-shaped glochidia.

The seven sections now recognized within the genus *Azolla* (see Fowler 1975, pp. 486, 488), are defined on the above parameters, i.e. float number and glochidia morphology. Apart from *A. barbata* (section Filifera), all multifloated species have anchor-shaped glochidia (section Kremastospora). Other anchor-shaped glochidia are found in sections Azolla and Trisepta, which have three and nine floats respectively.

Very little emphasis has been placed on megaspore wall structure in classification, although recent studies (Martin 1976*a*, *b* and Fowler and Stennett-Willson 1978) have paid more attention to this feature. It is still not clear how the wall structure may have been derived, and the present study has shown no trend in the stratigraphic occurrence of particular morphologies, nor any particular wall morphology consistently associated with a particular float number etc. More work is needed before the megaspore wall structure can be successfully used in phylogenetic interpretations.

The presence of a collar on a multifloated species is a new occurrence. This could, however, be interpreted in two ways: first, that multifloated forms with a collar gave rise to three- and nine-floated forms (also with a collar); and secondly, the collar may have arisen in three separate instances in multifloated, nine- and three-floated species.

Clearly, despite the extensive fossil record of *Azolla*, no clear idea of the evolutionary development within the genus is yet available. One major feature of note is that multifloated species became extinct by the end of the Eocene. However, two features previously known only in species with a small float number, namely the presence of a collar and a tendency towards a triseptate float zone, have now been shown to occur in an Eocene multifloated species. In a genus where five of the sections and nearly 90% of the species are fossil, and certain major variations in morphology (e.g. numerous floats) are known only from fossil species, the importance of the fossil record is self-evident. Within this record there are two important steps needed to extend our knowledge: the first is a reinvestigation of certain poorly described multifloated species, and the second an unequivocal answer to the controversy concerning the number of floats on the species *A. simplex*, *A. geneseana*, and *A. primaeva* (section Simplicispora).

CONCLUSIONS

Specimens of *Azolla* with numerous floats fall into one of four categories: 1, floats indistinguishable; 2, floats enmeshed loosely in a hairy weft, and thus able to shift their position with respect to the megaspore; 3, floats enmeshed in a hairy weft derived from a basal collar, thus forming a compact structure; and 4, floats in a compact structure held together by maniculae on the floats. This latter situation, described by Martin (1976*a*, *b*) has not been observed by other workers, and it seems possible that at least one species supposed to possess this feature may in fact have a diminutive collar. *A. montana* has a compact float arrangement (but no collar or maniculae), and this may be due to the development of a well-defined dome-shaped hair weft, as occurs in those species which do have a collar. *A. colwellensis* is the only species in category three above, and as such it may be considered one of the most adapted of the multifloated species. In addition, it is the only multifloated species with a tendency to trispetation of the float zone, and with a hairy exoperine. It is also the youngest multifloated species yet recorded.

Evidence of plasticity in float number in *Azolla* is afforded by the variation in float number in *A. colwellensis*, and by a specimen of *A. prisca* (usually with nine floats) with fifteen floats. It is concluded that float number is dependent on the number of abortive megaspores which are merged within each float. A theoretical maximum of twenty-four floats (one megaspore to each float), requires that seven abortive megaspores should be embedded in the perine of the mature megaspore. Any number of floats may occur, depending on the number of megaspores in each. No one float number need be derived from another number, but each may occur as an independent variation on this basic theme.

Megaspore wall structure, while emerging as a useful specific feature, is not yet well enough studied to be used in phylogenetic interpretations. Microspore massulae with anchor-shaped glochidia occur throughout the range of the genus, on multifloated, nine-, three-, and one-floated species. Their presence is probably related to the possession of an hairy megaspore surface in which they become entwined. As such a surface may be derived from two different parts of the megaspore apparatus, species with anchor-shaped glochidia need not be closely related. The significance of the presence of septae in the glochidia is not clear, *A. colwellensis* and *A. anglica* being the only multifloated species which possesses them.

The significance of *A. colwellensis* lies in demonstrating that a number of features previously known only from nine-, three-, or one-floated species, are now recorded in a multifloated species. This is also the youngest multifloated species known, being of Upper Eocene age. This new record may be seen as adding to the complexity of the record of the genus and supporting ideas that many different lineages may have been involved in the evolution of the genus *Azolla*.

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PRE-MIOCENE SEAGRASS COMMUNITIES IN THE CARIBBEAN

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ABSTRACT. Fossil seagrasses are rarely found in the geological record. Since their ancient distribution cannot be determined directly, it has to be inferred by examining the components which characterize seagrass communities. In this way it has been suggested that although seagrasses first appeared in the late Cretaceous, they did not reach the Caribbean until the Miocene.

Caribbean larger foraminifera of late Cretaceous to Oligocene age are discussed, and certain species belonging to the genera *Chubbina*, *Ayalaina*, *Yaberinella*, *Cyclorbiculinoides*, *Cyclorbiculina*, and *Peneroplis* are recognized as probable seagrass-dwellers. A new model for the Caribbean is proposed in which seagrasses first appeared in late Cretaceous times, and became widespread during the Eocene.

THE importance of seagrasses in trapping carbonate sediment and stabilizing ecological niches is well known, and has been carefully documented by a number of authors such as Scoffin (1970), and Brasier (1975). Whilst it is highly desirable that the former distribution of these plants be determined in space and time, this is unfortunately difficult. Seagrasses lack readily fossilizable parts, and their pollen has a thin or absent exine which makes preservation unlikely. Even when preservation has taken place, it is difficult to distinguish between marine grass parts and those from terrestrial or freshwater areas which have subsequently been transported into a marine environment. The ancient distribution of seagrasses therefore has to be determined by indirect approaches based on the biological and sedimentological features, which together characterize present-day seagrass communities.

Although it is generally accepted that seagrasses first appeared during the late Cretaceous, there is no agreement as to how widespread they were at this or subsequent times. Based on sedimentological evidence, Petta and Gerhard (1977) concluded that certain Campanian sediments in Colorado were probably fossilized marine grass banks, analogous to modern *Thalassia* beds. This suggestion later received support from Bretsky (1978) who pointed out that the bivalves present in these sediments were well adapted to living in a seagrass environment. By contrast, Brasier (1975) has given an account, based mainly on palaeontological evidence, whereby seagrasses did not reach the Americas and Caribbean regions before the Miocene. Records of larger foraminifera in the Caribbean seem to be inconsistent with such a hypothesis. Before entering into such a discussion it is first necessary to describe the way in which larger foraminifera can be used to reconstruct seagrass distributions.

FORAMINIFERA AS INDICATORS OF VANISHED SEAGRASSES

The value of using larger foraminifera to indicate previous areas of seagrasses has already been outlined by Brasier (1975) but some of the problems associated with this approach should, perhaps, be re-emphasized.

At the present day, a number of foraminifera are known to spend at least a part of their life, in some geographical areas, as epifaunas on the blades of seagrasses. These include *Peneroplis planatus*, *Amphisorus hemprichi*, *Sorites marginalis*, *Marginopora vertebralis*, *Archaias angulatus*, and *Cyclorbiculina compressa* (Bock 1969; Davies 1970; Brasier 1975; Steinker and Steinker 1976; pers. obs.). These forms all have a relatively large size, a complex endoskeleton and a discoidal shape, and it would seem highly likely that at least some morphologically similar species have shared a similar style

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in the geological past. Thus, in theory, it should be possible to map out the distribution of certain fossil species, and to equate these occurrences with the former distribution of seagrasses.

This approach is limited because it has not yet been demonstrated that these, or any other foraminifera, are *restricted* to living on seagrasses. Living specimens of most of the forms mentioned above have also been reported from sediment samples, although in most cases these sediments were within grass beds, or closely associated with them. Seasonal changes, resulting in changes in the abundance of seagrass, also affect the foraminiferal populations (Bock 1969; Hottinger 1977). Thus although Bock (1969) found sixty-six different benthonic species attached to *Thalassia* blades on the Florida Keys, only ten of these were abundant throughout the year.

Further complications arise because living forms which apparently prefer an epiphytic lifestyle, may have close relatives which are better adapted to different environments. Present-day examples are known where different species of the same genus, living in approximately the same area, apparently prefer different substrates (see, for example, Hottinger 1977). This is a common feature amongst many other groups of animals, and is often referred to as the Volterra-Gause principle. Even microspheric and megalospheric forms of the same species may occupy different environments (Walker 1976).

Other features which might be expected of fossil seagrass communities include highly diverse foraminiferal populations, as these are often associated with present-day marine-vegetated areas (Murray 1970; Steinker and Steinker 1976). By contrast the adjacent unvegetated areas tend to contain a less diverse fauna, a smaller percentage of mud-sized particles (Scoffin 1970), and may be the typical habitats for the spherical to fusiform alveolinids *Borelis* and *Alveolinella*. These two differing facies would be expected to occur as lateral equivalents in the fossil record.

The above discussion suggests that correlating fossil foraminiferal distributions with those of seagrasses will be subject to certain degrees of inaccuracy, ambiguity, and personal bias. Of particular importance is the scale on which such correlations are attempted. Over small areas there can be little hope of identifying seagrass localities using fossil foraminifera, but on a regional scale it should at least be possible to identify those areas which are consistent with the proposal that they contained fossil seagrass communities. This approach will now be applied to the Caribbean region.

RECONSTRUCTING FORAMINIFERAL DISTRIBUTION PATTERNS IN THE CARIBBEAN

Dilley (1973) and Hottinger (1973) have discussed some of the general problems involved in mapping ancient larger foraminiferal distributions, and in the Caribbean such problems are especially acute. Not only must the recorded occurrences be taken into account, but also the state of knowledge across the region. This point can be illustrated by considering Jamaica, which has a well-established Geological Survey and University Geology Department, together with a long history of palaeontological research (Chubb 1975). Despite the many previous studies, and the relatively small size of the island (11 420 km^2), four new genera and six new species of larger foraminifera have been described from the Middle Eocene deposits alone over the last ten years (Robinson 1969, 1974*a*; Eva 1976*b*). Clearly the faunas are not yet adequately described, and the situation elsewhere in the region is considerably worse. Critical areas such as Nicaragua or Hispaniola have had relatively few detailed investigations, and whilst forms may be equally diverse, published accounts are lacking.

It should also be remembered that marine sediments of Palaeocene and Oligocene age have not always been widely recognized in the region. In the former case this appears to reflect a real gap in the marine record (Khudoley and Meyerhoff 1971). The latter case, however, reflects the confusion that has arisen ever since Eames *et al.* (1960, p. 448) first declared that 'no Oligocene can be recognised in the marine sediments of the western hemisphere'. Although this position has been repeatedly refuted by later workers, a certain amount of confusion still surrounds the recognition of the Oligocene in the Caribbean, and this should be considered when discussing faunal distributions of this age.

Finally it will be noted that the foraminiferal distributions have been plotted onto a present-day map of the Caribbean (text-fig. 1*a*, *b*). This approach can only be justified because all present reconstuctions of the Caribbean–Central American region for Cretaceous or early Tertiary times remain highly controversial.

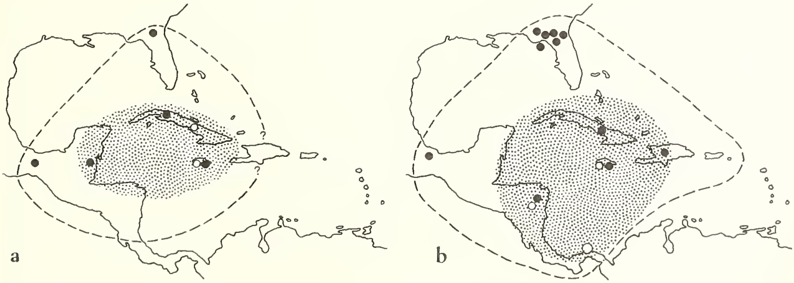
OCCURRENCES OF SELECTED LARGER FORAMINIFERA

Upper Cretaceous. Brasier (1975, p. 690) suggested that the genera *Vandenbroeckia*, *Broeckia*, *Edomia*, *Qateria*, and *Pseudedomia* might have been seagrass-adapted forms, and noted that their distribution was restricted to the Tethyan region. However, a number of similarly constructed porcellaneous forms were present in the Caribbean at this time (Dilley 1973; Robinson 1974*c*). These included species of the genus *Chubbina* which have an analogous structure to *Pseudedomia*, a lenticular to discoidal shape (Robinson 1968*b*), and which are known from Jamaica, Mexico, Florida, and Cuba (Hamaoui and Fourcade 1973). Another similar-shaped species is the peneroplid *Ayalaina rutteni* which has a thin-walled delicate test, and has been recorded from Jamaica and Cuba (Robinson 1968*b*).

These forms seem to be restricted to the northern Caribbean (text-fig. 1*a*), as opposed to the widespread development of the pseudorbitoids and orbitoids (Dilley 1973; Robinson 1974*c*). This probably indicates significant large-scale variations in the shallow-water facies of the Caribbean at this time. The greatest recorded faunal diversity in the carbonate shelf environment occurs in Jamaica, Cuba, and Belize; and these areas are tentatively correlated with the distribution of seagrasses (text-fig. 1*a*).

Palaeocene–Eocene. Marine Palaeocene sediments are poorly represented on the Caribbean islands (Khudoley and Meyerhoff 1971) but carbonate rocks of Eocene age occur across much of the region, and often contain abundant larger foraminifera.

Brasier (1975) placed great emphasis on the distribution of *Orbitolites* in reconstructing his distribution of Eocene seagrasses. The justification for this approach lies in the close structural similarity between *Orbitolites* and living species such as *M. vertebralis*, and *S. marginalis* which attach themselves to marine vegetation. This view was also shared by Hottinger (1973, p. 444) who suggested that *Orbitolites* 'lived probably epiphytic on plants like recent *Sorites*'.



TEXT-FIG. 1. Maps of the Caribbean showing the distributions of selected larger foraminifera for (*a*) late Cretaceous, and (*b*) Eocene times. In (*a*) solid circles represent species of *Chubbina* and open circles *Ayalaina rutteni*; in (*b*) solid circles represent species of *Fabularia* or *Borelis*, whilst open circles depict *Cyclorbiculinoides jamaicensis* or *Yaberinella jamaicensis*. The dashed lines contain the larger imperforate foraminiferal provinces as defined by Robinson (1974*c*, 1977). Areas that were probably inhabited by seagrasses are shaded. Sources of data are discussed in the text.

Although it is true that *Orbitolites* is unknown in the Caribbean, several closely related forms are present. These include *Cyclorbiculinoides jamaicensis*, which is widely distributed in the Eocene shelf carbonates of Jamaica (Robinson 1974*b*), and which is structurally so similar to *Orbitolites* that it was originally mistaken for it (Robinson 1968*a*). Other large peneropliform to discoidal species present in the shelf carbonates of Jamaica include *Yaberinella jamaicensis*, and a species belonging to a new genus, analogous to *Puteolina*, which has not yet been formally described. The palaeoecological position of *Y. jamaicensis* deserves attention, for although both Hottinger (1973) and Eva (1976*a*) have suggested a restricted back-reef environment for this species, it is now known from such widely spaced areas as Jamaica (Vaughan 1928), Panama (Cole 1952), and Nicaragua (F. Bourgeoise pers. comm. 1975). Whilst much still remains to be learnt about the ways in which larger foraminifera are dispersed, attachment to floating seagrasses is known to be an important and effective method (Bock 1969; Hottinger 1977). The size, shape, and distribution pattern of *Y. jamaicensis* are therefore all consistent with an epiphytic lifestyle.

If the discoidal-shaped species discussed above represent seagrass dwelling forms, we might also expect to find, in laterally equivalent strata, back-reef sediment dwellers similar to the present-day *Borelis*. Brasier (1975, p. 694) took this view, but argued that it was not until the Miocene that *Borelis* became 'the first alveolinid to reach the Neotropics'. This assertion deserves some comment. Cole (1941) and Levin (1957) have both recorded *Borelis* from Eocene deposits in Florida, and the genus has also been reported from Mexico (Butterlin and Bonet 1960), although none of these references is accompanied by unequivocal illustrations. However, the near-spherical alveolinids *Fabularia vaughani*, *F. verseyi*, and *Pseudofabularia matleyi* have been well illustrated, and are widely distributed in the inner shelf carbonates of Jamaica (Robinson 1974*a*, *b*; Eva 1976*b*). *F. vaughani* has long been known from Florida (Cole and Ponton 1934), and Wessem (1943) and Butterlin (1956) have also recorded the presence of alveolinids in the Eocene limestones of Cuba.

The lithology of the Eocene sediments in Jamaica is also consistent with the view that seagrasses were established by this time. The lower Eocene and lower Middle Eocene shelf deposits are characterized by lenticular bodies of highly fossiliferous limestone, 0·5–2·5 km in diameter, surrounded by well-bedded unfossiliferous quartzo-feldspathic sandstones and siltstones (Robinson 1969; Wright 1974). These sediments appear to be analogous to those which presently accumulate within the Salt River Estuary off St. Croix (Petta and Gerhard 1977). Here carbonate deposition is confined, and largely created and stabilized by, discrete areas covered by seagrasses and their associated faunas. The surrounding areas are carbonate deficient, and consist of terrigenous muds deposited by the Salt River. The younger Eocene shelf sediments in Jamaica consist predominantly of poorly sorted biomicrites, which although not indicative of fossil seagrass beds, are certainly consistent with such possible palaeoenvironments.

The presence of seagrasses in the Caribbean by Eocene times therefore seems quite likely although the extent of its distribution is less certain. Faunas are most diverse in Jamaica, Cuba, and Nicaragua, but the presence of *Y. jamaicensis* in Panama suggests that seagrasses may have been extending southwards. Areas of relative carbonate stabilization are also reflected in the distribution of mangroves, and it seems significant that *Pelliceria* and *Rhizophora* are known from both Jamaica and Panama at this time, but appear to be absent from Florida (Graham 1977). The larger foraminiferal faunas in Florida are clearly impoverished compared with Jamaica (Robinson 1974*c*), suggesting that seagrasses did not reach so far north, or that they were only poorly developed (text-fig. 1*b*).

Oligocene. During the Upper Eocene many larger foraminifera became extinct, leaving several niches vacant, which were not always immediately reoccupied. In the Caribbean this is exemplified by the disappearance of the possible seagrass-dwellers *Y. jamaicensis* and *Cyclorbiculinoides jamaicensis*, and also by probable sediment-dwelling genera such as *Fabularia*, *Pseudofabularia*, and *Keramosphaera*. Although the latter niche appears to have been quickly occupied by species such as *Archais angulatus* (McFarlane 1977; Seiglie *et al.* 1977), and *Fusarchais bermudezi* (Reichel 1952), possible seagrass-dwelling forms are uncommon. They may, however, be represented by species such as

Peneroplis proteus, *Puteolina* sp., and *Cyclorbiculina* sp., which are known from the islands of the Greater Antilles (McFarlane 1977; Seiglie *et al.* 1977).

Miocene–Recent. Evidence for the presence of seagrasses in the Caribbean during this time has been discussed by Brasier (1975), and need not be further elaborated.

CONCLUSIONS

Although there are a number of difficulties inherent in any attempt to analyse the distribution of fossil foraminifera in the Caribbean, it is clear that even the present evidence is inconsistent with the model proposed by Brasier (1975).

Exactly when seagrasses appeared in the Neotropics in unclear, but the late Cretaceous forms are diverse, and in *Ayalaina rutteni* and species of *Chubbina* there is the suggestion of seagrass-adapted forms. The Eocene deposits of the region are most studied, and their larger foraminifera and sediment type almost certainly indicates the presence of seagrasses by this time.

Present evidence therefore suggests that the establishment of seagrasses in the Caribbean followed similar lines to that in the Tethyan region. Hopefully this proposal will encourage workers to seek further evidence for fossil seagrass communities in the Caribbean. Future work must involve not only studies of foraminiferal distributions, but also detailed sedimentological studies, and searches for fossil remains of the plants themselves.

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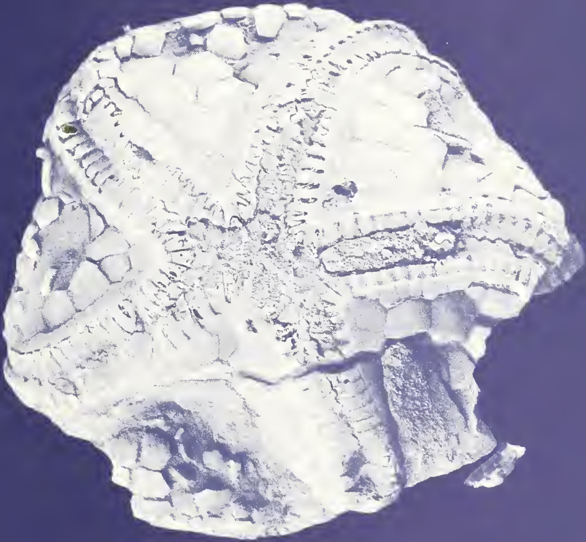

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Specimen in the Smithsonian Institution; photograph by H. B. Whittington.

SCULPTURE AND MICROSTRUCTURE OF THE EXOSKELETON IN CHASMOPINID AND PHACOPID TRILOBITES

by LEIF STØRMER

ABSTRACT. This paper describes the detailed skeletal anatomy of chasmopinid trilobites from the Ordovician of the Oslo region, and *Phacops* from the Polish Devonian. Lamination of the cuticle is similar to that previously reported, and the outermost prismatic layer has been conclusively proved. Several types of tubercles or pustules on the surface of the exoskeleton have been identified, for which a classification is proposed. Canals through the exoskeleton range from about 1–40 μm in diameter. In *Chasmops* spp. apparently smooth tubercles have a thin central canal through the outer zone changing downwards into a wide canal. This smooth tubercle organ shows some resemblance with the sensory campanular organ (mechanoreceptor) in Recent arthropods. Sections of the big composite tubercles or pustules in *Phacops* have revealed two sets of ducts, partly with different directions: (1) numerous close-set fine (4 μm) canals in a fan-like arrangement, and (2) diffuse ramifying branches or tubes with distal bundles of tubules, the blunt terminals of which are inserted into the lower surface of the outer zone of the exoskeleton. This internal tubules organ might possibly, in general features, be analogous with the much smaller campanular organ in the halteres in Diptera. Just below the prismatic layer there are numerous small (10–20 μm) subsphaeric cavities apparently connected with the epidermis by a single thin (1·5–2·0 μm) perpendicular canal, which are termed Osmolska cavity organs.

There is a considerable variation in muscle-scar pattern. Some species have calluses on the inner surface corresponding to shallow pits on the outer surface. Similar pits and dark patches, and knobs or calluses on the inner surface of the exoskeleton, are scars or small apodemes of muscles leading from the dorsal exoskeleton to the presumed thin membrane representing the ventral body wall inside the marginal doublure.

THIS paper was planned to form a part of a monograph on the subfamily Chasmopinae of the Middle and Upper Ordovician of the Oslo Region. As the work proceeded, some of the characters which had to be studied in greater detail, for example in thin sections, were relevant to general problems of trilobite morphology and anatomy. These characters comprise the sculpture and microstructure of the exoskeleton, the relations between the hypostoma and cephalic appendages, and finally a possible distinction of exuviae and dead individuals based on the thickness of the exoskeleton.

MATERIAL AND METHODS

With few exceptions the specimens studied belong to the Middle Ordovician of the Oslo Region. In this area the Chasmopinae play an important role as guide fossils. In addition to the Norwegian material a few specimens from Estonia have been borrowed from the British Museum (Natural History) and from the Naturhistoriska Riksmuseet in Stockholm; the Polish *Phacops* specimens were presented by Dr. Osmolska.

The Norwegian specimens of the Chasmopinae are usually well preserved in limestones, either in massive beds or in nodules in shales. The relatively few specimens preserved in shale have provided good imprints of the surface sculpture. The limestone specimens are often considerably recrystallized preventing the preservation of the minute internal structures.

The preservation of the fine structural details varies in the material examined. In general it seems that specimens from Ringerike, Hadeland, and the Mjøsa areas are best for detailed studies. The good preservation of structural details is to a large extent dependent on the presence of fine-grained pyrite, as in well-preserved specimens of *Tretaspis* (Størmer 1930). The outer surface sculpture of the

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Chasmopinae is mostly provided with various kinds of prominent tubercles or pustules. Since the inner surface is usually smooth, exoskeletons almost always split off along the inner surface leaving the outer surface unexposed. Most published illustrations of chasmopids are of internal moulds. The outer sculptured surface might occasionally be seen in weathered counterparts. The external surface in limestone specimens has to be studied in thin sections.

Most of the photographs of the surfaces of specimens or casts shown on the reproduced photographs were made from material covered with 'opaque' and ammonium chloride. All specimens and thin sections, with the exception of a few from British Museum (BM) and the Riksmuseum in Stockholm (RMS), belong to Paleontological Museum (PMO) of the University of Oslo.

LAMINATION OF EXOSKELETON

Microstructure of the trilobite exoskeleton has been much studied recently (Miller 1975; Osmolska 1975; Teigler and Towe 1975; Miller 1976, Dalingwater and Miller 1977). The recent results have been based mainly on Ordovician asaphids and Devonian phacopids. The structures studied mainly comprise the lamination of the exoskeleton, the surface sculpture, and the associating canals or ducts.

Among recent arthropods the cuticles of insects and decapod crustaceans are the best known. Although the arthropods have much in common, a complete conformity in structures is not present. According to current terminology the following units might be distinguished in the exoskeleton: (1) A very thin (around 4 μm) external epicuticle with very little or no chitin, (2) a thick procuticle, containing chitin, comprising: (2*a*) an outer hard and rigid exocuticle resulting from an impregnation by quininetanned proteins (in crustaceans and diplopods by calcareous substances), and (2*b*) an inner, more flexible, endocuticle. Dennell (1960, p. 456) divides the exoskeleton into an epicuticle and an endocuticle (which involves a different meaning of the latter term). The endocuticle comprises an outermost pigmented layer, a middle calcified layer, and lower uncalcified layer above the epidermis.

In trilobites the textural subdivisions of the exoskeleton has, among others, been described and discussed by Cayeux (1916), Størmer (1930), and more recently by Dalingwater (1973), Teigler and Towe (1975), and Dalingwater and Miller (1977). Teigler and Towe distinguished two layers in most of the species they examined. (1) a thin (20–30 μm) outer pigmented layer which might be prismatic in structure and is supposed to be composed of calcium phosphate, (2) a principal layer composed of calcium carbonate. In *Tretaspis* Størmer (1930, pl. 12, fig. 1) described a thin (20 μm) external pigment layer and a similar structure was noticed by Kielan (1954, p. 41). However, Miller (in Dalingwater 1973, p. 836) interpreted the pigment layer as a dense micritic envelope due to attack by foreign organisms. The variation in thickness might to some extent support this view, but the pigment layer seems to be confined to the outer surface only. Micritic envelopes would be expected to occur on both sides of fragments of the exoskeleton. In *Asaphus raniceps* Dalingwater and Miller (1977, p. 24, text-fig. 2) have been able to distinguish a principal layer comprising three laminate zones below a thin outermost layer. This outer layer would correspond to what has been described as the prismatic layer. The four units of the exoskeleton which we recognize are: (1) outer prismatic layer, (2) outer laminate zone, (3) central laminate zone, (4) inner laminate zone.

The thickness of the prismatic layer is not determined by the authors mentioned, but the outer laminate zone comprises up to one-fifth of the total thickness of the cuticle (less in the cephalon). The narrow laminar units of this zone are around 5 μm thick. The central and most prominent zone (50–70 μm) with 4–5 μm wide laminar units occupies around three-fifths of the total thickness. The zone grades into the relatively thin inner laminate zone, which has narrow laminar units similar to those in the outer zone, and is variable in thickness.

1. *Prismatic layer*

In most specimens examined this thin outermost layer is not preserved, but we can see this layer in *Phacops granulatus* and a few chasmopinids. One of the reasons for the lack of preservation of the prismatic layer is probably due to the perforation of the layer by Osmolska cavities just below the prismatic layer. The prismatic layer and half of the layer with the cavities tends to break off at this level (text-fig. 6*c*). In a well-preserved specimen of *Toxochasmops* sp. from the Hamar District (Pl. 29, fig. 7*a*, *b*; text-fig. 9*a–c*) a thin (7–8 μm) layer outside the level with the Osmolska cavities, represents the prismatic layer. Traces of an outermost thin (5–6 μm) layer are seen in a thin section of *Chasmops* sp. nov. D (Pl. 29, fig. 2). The layer seems to be partly penetrated by the upper part of some of the Osmolska cavities.

In the *Phacops* specimens figured by Dalingwater (1973, pl. 109, fig. 2), Osmolska (1975, pl. 1, figs. 11–13), and Miller (1976, pl. 2, figs. 3, 4) the outer prismatic layer seems to have been completely worn off, possibly during the preparation of the specimens. The thin sections of *P. granulatus* shown here are better preserved and clearly show the prismatic layer (Pl. 30, figs. 3*b*–7; Pl. 31, figs. 1*a*–4; text-fig. 5*a–e*). The SEM photographs in particular show the outermost layer with the prisms (Pl. 34, figs. 1*a*, *b*, 7*a*, *b*). The thickness of the prismatic layer is about 8–10 μm, the exposed sides of the prisms about 2 μm. It is not possible to decide whether or not the layer is penetrated by minute canals ascending from below.

2. *The outer laminate zone*

In *Tretaspis* (Størmer 1930, pl. 12, fig. 1) this zone might be represented by a 20 μm-thick pigmented layer comprising about one-sixth to one-seventh of the total thickness of the exoskeleton. A relatively thin outer laminate zone seems also to be characteristic of the Chasmopinae. In a well-preserved large specimen of *Toxochasmops extensus extensus* (Pl. 25, fig. 1*a*, *b*), the outer laminate zone has a thickness of 30–40 μm representing about one-tenth of the exoskeleton. However, the lamination of the zone is not preserved and the boundary towards the central zone is not distinct. Fine lamellar units are only indicated in the tubercles (Pl. 25, figs. 3, 5*a*, *b*; Pl. 28, figs. 1, 2, 4*a*, *b*, 6), where they appear as sloping lamellae parallel to the outer surface of the lobes and cones. The distance between these laminae is only about 5 μm. The lamination of the tubercles might form a continuation of laminae of the remaining zone. In *C.* sp. nov. A (Pl. 25, fig. 5*a*, *b*; Pl. 28, figs. 4*b*, 5*b*) the lamination of the tubercles and their bases indicate that the outer laminate zone was relatively thicker than in *Toxochasmops*, comprising as much as almost half the thickness of the exoskeleton.

In *P. granulatus* zonation of the exoskeleton is normally not clear (Pl. 30, figs. 1*a*–2*b*; Pl. 31, fig. 3). The light zone above the tubules in the composite tubercles may belong to an outer (laminate) zone. In one of the SEM photographs (Pl. 34, fig. 3) an outer zone, 80 μm wide, is marked off from the rest of the exoskeleton. Traces of zigzag or parabolic structures are faintly indicated. In Recent decapod crustacea Mutvei (1974, fig. 1) has demonstrated vertical lamellae with a parabolic cross-section, connecting two horizontal lamellae of the exoskeleton. Towe (1978) notes the apparent lack of such structures in trilobites. Towe has suggested to me that the present structures are impressions of rhombohedral calcite crystals rather than primary parabolic structures.

3. *The central laminate zone*

The prominent laminar units of this zone are shown in the large specimen of *T. extensus extensus* (Pl. 25, fig. 1*a*, *b*, also Pl. 25, fig. 4). The laminar units consist of very thin (a few μm thick) laminae and much thicker (20–30 μm) interlaminae about seven in number. The outermost laminar unit is thinner than the rest and might represent a transition to the outer laminate zone. The central zone grades without any distinct boundary into the inner laminate zone. The thickness of the central zone in the specimens mentioned is about 220 μm which amounts to two-thirds the thickness of the exoskeleton. A thin section across the gena of the same subspecies (Pl. 25, fig. 2*a*, *b*) preserves the laminate structure in two small patches only. It is interesting that these patches occur just below small depressed smooth areas without tubercles or Osmolska cavities. The smooth depressed areas are evidently the genal muscle scars described below. It is possible that the absence of canals through these scars and the possible presence of some special organic compound in connection with the muscle fibrils (tonofibrils), might have caused the favourable preservation of the lamellar structure. The lamellar units tend to form dark and light bands (Pl. 25, fig. 2*a*) rather than thin laminae and thick interlaminae as in Plate 25, fig. 1*a*. The structures resemble those described by Dalingwater and Miller (1977, text-fig. 2) in *A. raniceps* and in *Tretaspis seticornis* by Størmer (1930, pl. 12, fig. 1; text-fig. 41*b*). In the first species the number of laminar units is four to five, in the latter apparently seven.

4. *The inner laminate zone*

All three laminate zones are not preserved at the same time, usually only one zone is well preserved while the details of the other are evidently obliterated by recrystallization. A recrystallization of the inner zone is demonstrated in *Tretaspis* (Størmer 1930, pl. 12, fig. 4) and indicated in polarized light in *Chasmops* sp. nov. A (Pl. 25, fig. 5*b*). The lamination of the zone is demonstrated in *Toxochasmops extensus extensus* (Pl. 25, fig. 1*a*, *b*), in *T. extensus* subsp. nov. (Pl. 25, fig. 3) and in *C.* sp. nov. A (Pl. 25, fig. 5*a*, *b*). The lamellar units have a thickness of about 10 μm which is about half that of the central laminate zone. Around eight lamellar units seem to be present. The zone has a thickness of 90–110 μm in the *Toxochasmops* specimens and 90 μm in *Chasmops*, which comprises about one-third of the exoskeletal thickness. Since the inner part of the exoskeleton might be partly resorbed before molting, the thickness might be expected to vary.

In a thin section of *C. odini* from Estonia, a layering of the cephalic exoskeleton is indicated at the steep anterior border (Pl. 29, fig. 6). The laminar units are not very distinct and there seems to be a gradual transition between the central and inner (upper in section) more finely laminated zone. An outer zone is not marked off, but must have been thin. In the central zone the maximum thickness of the laminar units is 55 μm which is one-tenth the total thickness of the exoskeleton at this place. An inner zone separated from the central zone is faintly indicated in some of the SEM sections of *P. granulatus* (Pl. 34, figs. 4, 6).

Since Trinucleidae, Asaphidae, and Chasmopidae are not closely related a largely common type of structure of the exoskeleton in trilobites is suggested. As pointed out by Dalingwater and Miller (1977, p. 30, pl. 10, fig. 4) and by Størmer (1930, p. 99, text-fig. 41) the structures observed are similar to those of the exoskeleton in decapod crustaceans. However, the similarities do not need to imply any closer phylogenetic relationships.

EXPLANATION OF PLATE 25

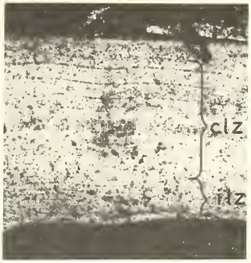
Figs. 1*a*, *b*, 2*a*, *b*. *Toxochasmops extensus extensus* (Boeck, 1838). 1*a*, perpendicular section of cephalic exoskeleton; 1*b* in crossed nicols. Lamination of thin outer laminate zone not preserved. 4bδ, E. Rauskjær, Asker, PMO 94416, × 100. 2*a*, *b*, section across the gena near the eye. Dark colour due to tonofibrillae in exoskeleton below genal depressions. Tubercles of granule type and Osmolska cavities on outer surface between depressions. 4bδ, E. Rauskjær, Asker, PMO 94416, 2*a* × 50, 2*b* × 100.

Fig. 3. *Chasmops* sp. nov. A. Perpendicular section of cephalic exoskeleton showing tubercles of granule type with 'christmas-tree' lamination and laminated inner zone. 4*a*, Vollen, Asker, PMO 94398, × 104.

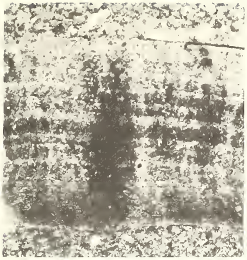
Fig. 4. *Toxochasmops extensus* subsp. nov. Perpendicular section across lateral (?) border, either dorsal skeleton or doublure. Pyrite impregnation. Light narrow layer at inner border. 4bγ, Vestbråten, Røyse, Ringerike, PMO 69349, × 170.

Fig. 5*a*, *b*. *Chasmops* sp. nov. A. Perpendicular section of cone type of tubercle with 'christmas-tree' lamination. Central canal not in section; *b*, crossed nicols distinguishing dark inner laminate zone. 4aβ, Vollen, Asker, PMO 94398, × 104.

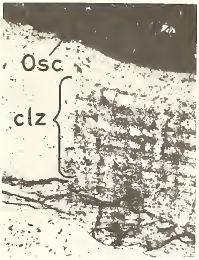
clz = central laminate zone, *gede* = genal depression, *gtu* = granule type of smooth tubercle, *ilz* = inner laminate zone, *Osc* = Osmolska cavity.



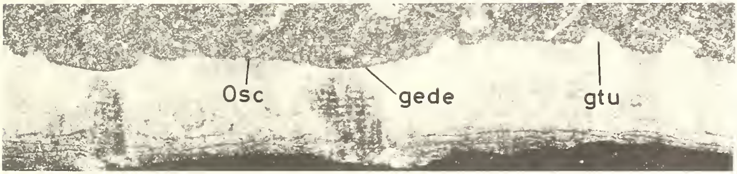
1a



1b



2a



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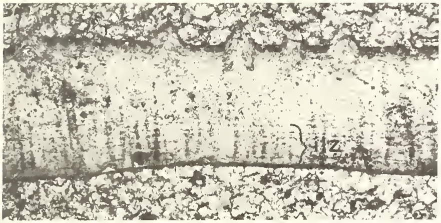

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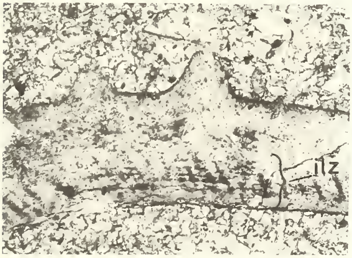
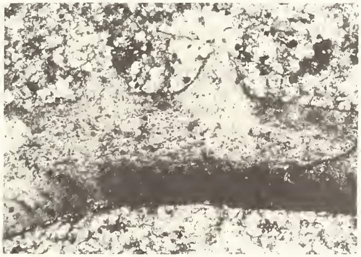
4



5a



5b

STØRMER, trilobite microstructure

TUBERCLES AND ASSOCIATED INTERNAL STRUCTURES

In Recent arthropods the external solid surface is usually provided with various kinds of pustules, tubercles, scales, and spines as well as numerous perforations leading into canals through the exoskeleton. However, even in Recent forms the function of the various structures are little known (Grassé 1975).

Terminology. Among the various types of sculptural elements, the tubercles or pustules are the most common in trilobites. Following the current practice the term tubercle is applied although the term pustule might seem more appropriate in several cases. Segury (1967) defines the term tubercle as a round lobe of variable size protruding from some part of the body or from an organ or from a duct. According to this definition the term tubercle comprises many different structures and functions. Kennaugh (1968) uses the term for several different structures, evidently with different functions, in three species of Ricinulei among Recent arachnids. In describing the sculpture or ornamention in trilobites Harrington, Moore, and Stubblefield (1959) use the term tubercle in a broad morphological sense. Because of the particular internal structures of the large tubercles in species of *Phacops*, Miller (1976) suggests the term 'pseudotubercle' for this type of tubercle. I agree that this type of tubercle is unique, but since the morphology of the tubercles is so important in taxonomic descriptions of trilobites, I prefer to use the general term tubercle also for the special tubercles in *Phacops*.

The following morphological types of tubercles are distinguished here.

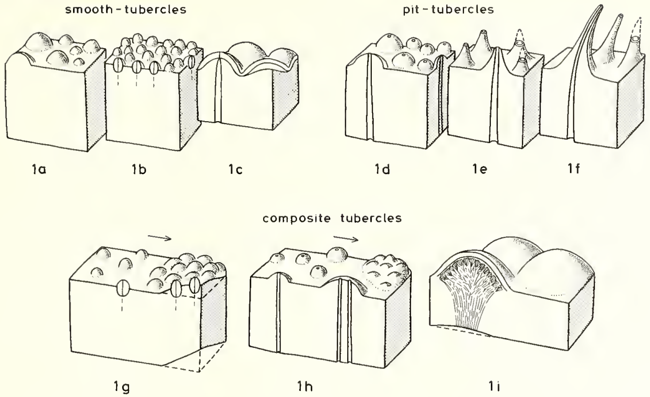
1. *Smooth tubercle*. Circular to subcircular discrete lobe without discernable apical pit or pits. Dimensions small to large.
   Ordinary type (text-fig. 1*a*). Circular tubercle or lobe. Small to medium size.
   Granule type (text-fig. 1*b*). Small circular hemispheric tubercle, convex at the top. Often appearing in great numbers forming a continuous granulate surface. Small size. Height 35–45 μm, width at base 70–80 μm.
   Low convex type (text-fig. 1*c*). Circular convex, mostly low, tubercle. Medium to large size.

2. *Pitted tubercle*. Circular discrete lobe of various shape with apical pit. Small to medium size.
   Ordinary type (text-fig. 1*d*). Lobe-shaped mostly hemispheric tubercle. Small to medium size.
   Cone type (text-fig. 1*e*). High cone-shaped tubercle with upper part often broken off. Medium size.
   Spine type (text-fig. 1*f*). Spine- or thorn-like tubercle. Small to large size.

3. *Composite tubercle*. Discrete or less discrete, mostly circular lobe or mound developing into flat pustule with steeper sides. Medium to very large size.
   Fused smooth tubercle type (text-fig. 1*g*). Circular lobe composed of more or less fused smooth tubercles of granule type often appearing as a dome. Medium to large size.
   Fused pit-tubercle type (text-fig. 1*h*). Circular lobe composed of more or less completely fused pit-tubercles of ordinary type. Small to medium size.
   Phacopid type (text-fig. 1*i*). 'Pseudotubercle' of Miller (1976). Circular to subcircular lobe, convex or flattened with steeper borders. Indications of fine lateral apertures might be distinguished. Large to very large size.

On the *inner* surface of the cephalic exoskeleton tubercles in the shape of calluses or pads may be present, as described later. The terms and definitions mentioned above are based on the external morphology only. The internal structures present additional information on the various types of tubercles, which bear on their possible functions. Many transitional stages exist between the different types of tubercles, but the proposed classification should prove useful both to morphological and taxonomic studies.

Highly sculptured specimens with cone and spine tubercles have to be studied in thin section, but in some cases casts of counterparts demonstrate the sculpture (Pl. 27, fig. 6). Where the outer surface is covered by closely packed low tubercles the details can be exposed (Pl. 26, figs. 1*a*, *b*, 4*a*, *b*; Pl. 27, figs. 1–5; Pl. 32, figs. 4, 7, 9, 10; Pl. 33, figs. 1, 4). Whether or not the external surface of the exoskeleton is observed often depends on the degree of external spinosity.



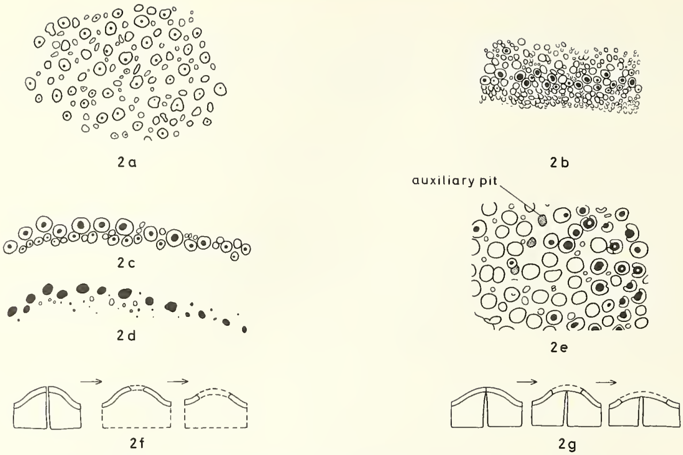
TEXT-FIG. 1. Diagrams of tubercles and spines on the cephalic exoskeleton: *a*, smooth tubercle of ordinary type; *b*, granule type with thin vertical canal preserved in upper onion-shaped portion only; *c*, low convex type, probably with a very thin central canal through upper layer and wide canal below; *d*, pitted tubercle of ordinary type with central canal, widening downwards; *e*, cone type, often with upper part broken off; *f*, spine type, often broken off; *g*, composite tubercle of fused smooth tubercle type. Arrow indicates transition from single to composite tubercle; *h*, fused pit-tubercle type. Arrow indicates transition from single to composite tubercles. *i*, Phacopid type.

Smooth tubercles

Granule type. These small tubercles have been studied in detail in *T. extensus extensus* and *T. extensus* subsp. nov. where they are very common. On exposed surfaces (Pl. 27, figs. 1, 2*a*, *b*, 5; Pl. 32, figs. 7, 9, 10) the tubercles appear as convex, more or less hemispherical nodes. This form is characteristic of the granules surrounding the lenses of schizochral eyes in many phacopid species. In thin sections (Pl. 25, figs. 2*a*, 3; Pl. 28, figs. 1, 2, 3) the upper part is convex, the lower part may form a part of a short cone (text-fig. 1*b*).

The height of the granule tubercle in *T. extensus extensus* and *T. extensus* subsp. nov. is around 35–45 μm. The tubercle is pierced by a central canal with a diameter around 2 μm (Pl. 28, figs. 1, 2). A cross-section of the duct is visible in one section (Pl. 28, fig. 3). A small opening at the summit is indicated only in thin section, hence its classification with the smooth group. Below the surface the granule tubercle is extended into an onion-shaped sac-like structure (Pl. 28, figs. 1, 2), distinguished in crossed polars (Pl. 28, fig. 2) by its lighter colour than the surrounding exoskeleton. The sack has radially sloping laminae forming in section a 'Christmas tree structure'. As noted above, the laminae might represent the outer laminate zone of the exoskeleton. The central canal does not continue further through the exoskeleton than the sac-like structure.

Low convex type. According to the present definition, this type occurs in *Chasmops* sp. nov. B (Pl. 26, fig. 1*a*, *b*; Pl. 32, fig. 4). The size of the relatively low tubercles varies with the size of the specimen, from about 130 μm to about 230 μm. In between these tubercles smaller ones of the granule type often occur. Some of the larger tubercles are partly abraded or worn off as shown also in text-fig. 2*e*. They vary from a convex surface or with a small opening at the summit, to one with a broad crater-like



TEXT-FIG. 2. Preservation of tubercles: *a*, Pitted tubercles of ordinary type, × 15, from glabella of *Flexicalymene*; *b*, tubercles partly abraded at the apex, × 15, from border of hypostoma of *Holia*; *c*, pit-tubercles, × 20, from border of pygidium of *Flexicalymene*; *d*, large 'openings', × 20, interior view of same silicified pygidium as in fig. 2*c*. The middle and inner zone were probably not silicified and therefore not preserved (Fig. 2*a*, *c*, *d* are based on Pl. 10, fig. 1; Pl. 9, figs. 15, 16 in Evitt and Whittington, 1953, fig. 2*b* on Pl. 21, fig. 5 in Whittington and Evitt, 1954); *e*, smooth tubercles of low convex type displaying various stages of abrasion, × 8·2, from glabella of *Chasmops* (Pl. 32, fig. 4); *f*, diagram of presumed abrasion of pit-tubercles in *Flexicalymene*; *g*, the same in *Chasmops*.

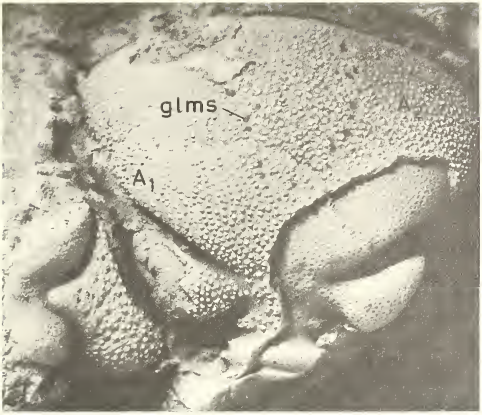
EXPLANATION OF PLATE 26

Fig. 1*a*, *b*. *Chasmops* sp. nov. B. *a*, glabella with fixigena on left side. Sculptured outer surface with glabellar muscle scars (auxiliary pits) removed posterolaterally exposing impressions of canal openings on internal mould, × 9; *b*, detail showing smooth tubercles of low convex type to the left and impressions of canal openings on the internal mould to the right, × 20. 4bα (?) Tønnerud, Hadeland, PMO 57698.

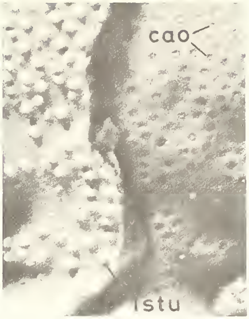
Figs. 2*a*, *b*, 3. *Toxochasmops extensus extensus* (Boeck, 1838). *a*, internal mould of median portion of glabella, cephalic length = 21 mm. In front impressions of a pair of calluses serving as muscule apodemes. Elsewhere impressions of canal openings, × 3; *b*, details of impressions of canal openings, × 25. 4bδ (16·10 mm below 4*c*), Ranskjær, Asker, PMO 94410, × 25. 3, larger specimen from same locality (length of cephalon = 31 mm). Details of impressions of canal openings. PMO 94411, × 25.

Fig. 4*a*–*c*. *Chasmops* sp. nov. C. *a*, posterolateral angle of cephalon with facial suture in facial suture furrow. Upper left internal mould exposed. Outer surface, except in occipital and marginal furrows, provided with different sizes of pit-tubercles of ordinary type, × 9; *b*, details of pit-tubercles (photographed upside down), × 25; *c*, impressions of canal openings with dark genal muscle scars in between, × 25. 4bα, Bratterud, Røyse, Ringerike, PMO 68615.

A_1–A_2 = location of thin section Pl. 28, figs. 4, 5. *cao* = canal opening, *fs* = facial suture, *fsf* = facial suture furrow, *gems* = genal muscle scar, *glms* = glabellar muscle scar (auxiliary pit), *1p*–*3p* = lateral glabellar lobes, *ocf* = occipital furrow, *pt* = apical pit, *lstu* = smooth low convex tubercle.



1a



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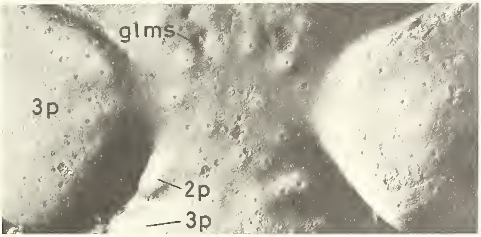

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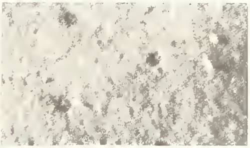

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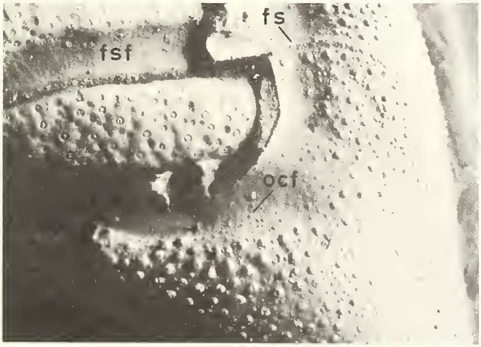

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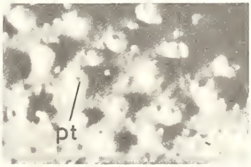

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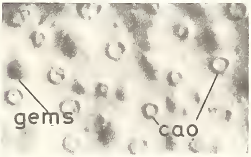


4c

STØRMER, trilobite sculpture

appearance. Crater-like forms are shown on Plate 32, figure 4. These different appearances are due to wear.

In the trilobites *Holia* and *Flexicalymene* Whittington and Evitt (1954, pl. 21, fig. 5) and Evitt and Whittington (1953, pl. 9, figs. 15, 16) found openings along the border of the cephalon and hypostoma which they interpreted as larger perforations surrounded by raised rims. The perforations were supposed to be the site of hairs of setae. Since 'craters' and tubercles without openings appear side by side, as in our Plate 32, figure 4, I interpret the American 'sockets' as due to abrasion. However, there is one difference. While in *Chasmops* sp. nov. B an outer thin layer is obviously abraded leaving smooth convex surface below, the wide openings in *Holia* pass right through the preserved exoskeleton and appear (text-fig. 2*c*, *d*) to be wider on the inner than on the outer surface. It seems possible that only the outer layer of the exoskeleton might have been silicified. The large inner opening would then correspond to the concave inside of the outer layer (text-fig. 2*f*).

In well-preserved specimens of *Chasmops* sp. nov. B showing the tuberculated outer surface and the internal mould side by side (Pl. 26, fig. 1*a*, *b*), there are impressions of prominent canals on the internal mould while the convex tubercles on the outside show no signs of canal openings. The wider canals belong to the deeper portion of the exoskeleton and become very narrow towards the outer surface. A thin section across the frontal lobe of the same specimen (Pl. 29, figs. 4, 5) clearly shows the prominent vertical canals with a diameter of around 24 μm through most of the thickness of the exoskeleton. One canal (fig. 5, left) seems to reach the outer surface. However, in another part of the section (fig. 4, right) the outermost short portion of the canals seems to be quite narrow, such as in the granule type of the smooth tubercle where the tiny apical aperture is not visible on exposed surfaces. The outer portion of the tubercle may have been subject to variable abrasion. The low convex tubercle of *C.* sp. nov. B has an apparently smooth surface, with a thin central canal running downwards through an outer layer which might correspond to the outer laminate zone. We do not know whether an outermost prismatic layer was penetrated by the fine canal. At the base of the presumed outer laminate zone the thin canal rapidly widens into a prominent canal running downwards through the central and inner laminate zones, flaring slightly at the inner surface. As shown below, the structures indicated in the reconstruction (text-fig. 1*c*) somewhat resemble certain campanular organs in Recent arthropods (text-fig. 7*b*).

EXPLANATION OF PLATE 27

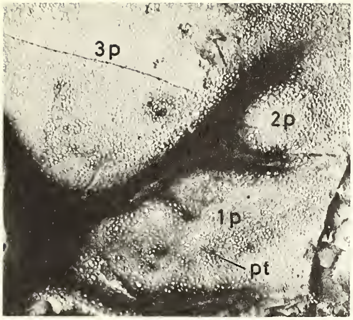
Fig. 1. *Toxochasmops extensus* subsp. nov. 4bγ, Vestbråten, Røyse, Ringerike, PMO 69345, ×9. Posterior left portion of glabella, granulation consisting of close-set smooth tubercles of granule type. A few larger pits might be sockets of setae.

Figs. 2*a*, *b*, 5. *Toxochasmops extensus extensus* (Boeck, 1838). 2*a*, detail showing small glabellar lateral lobe 2p and parts of large lateral lobe 3p. Lobes covered with granule type of smooth tubercles which also cover the low less discrete composite tubercles; 2*b*, front, internal mould with imprints of calluses with muscle scars, further back, outer surface with corresponding muscle scars between granules and composite tubercles. 4bβ–γ, Road section, Volla, Gran, Hadeland, PMO 68434, ×9. 5, anterior median portion of glabella with row of pits representing muscle scars on the outer surface and pits on the internal moulds representing calluses on the inner surface. Granules and composite tubercles, 4bδ, PMO 105705, ×9.

Figs. 3*a*–*c*, 4. *Toxochasmops* sp. nov. 3*a*, left anterior portion of glabella with two sizes of tubercles, some of the larger ones with one or two pits; 3*b*, posterior portion of glabella with discrete composite pit-tubercles surrounded by small ordinary pit-tubercles; 3*c*, details of small ordinary pit-tubercles between discrete composite pit-tubercles. 4bγ, PMO 20650, 3*a*, 3*c* ×9, 3*b* ×29. 4, less discrete composite tubercles with distinct elements, but without pits. 4bγ, Vestbråten, Røyse, Ringerike, PMO 68615, ×6.

Fig. 6. *Chasmops* sp. nov. A. Cast of right glabellar lobe, with ordinary pit-tubercles (perhaps some broken tubercles of the cone type) and simple composite pit-tubercles. 4bα, Road to Tangen, Semsvann, Asker, PMO 94403, ×19.

cotu = composite pit-tubercle, *gtu* = granule tubercle, *glms* = glabellar muscle scar or auxiliary pit, 2p, 3p = second and third lateral glabellar lobes, *pt* = pit, *pttu* = pit tubercle.



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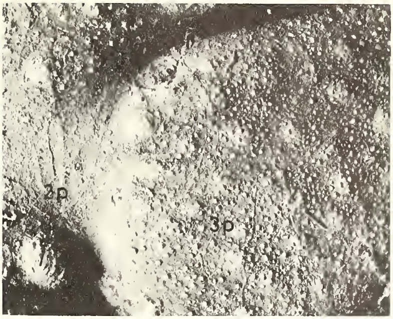

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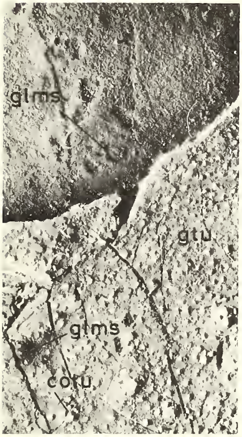

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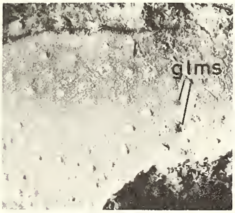

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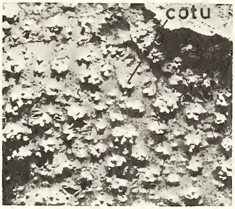

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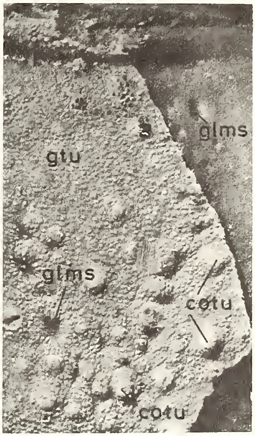

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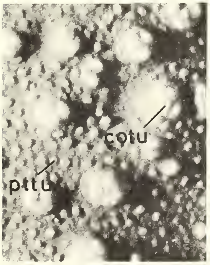

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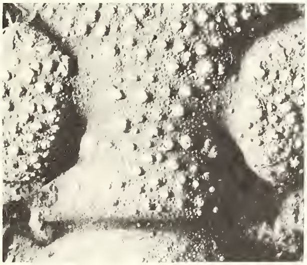

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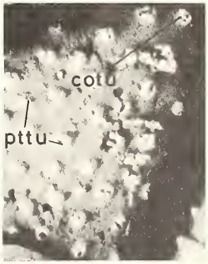

6

STØRMER, trilobite sculpture

Pitted tubercles

Ordinary type (text-fig. 1*d*). The ordinary type of the pitted tubercle is seen in *Chasmops* sp. nov. C (Pl. 26, fig. 4*a*, *b*), in *C*. sp. nov. A (Pl. 27, fig. 6), and in *Toxochasmops* (Pl. 27, fig. 3*c*). As in *Flexicalymene* (text-fig. 2*a*) the size of the ordinary pit-tubercle varies considerably. The internal mould of *Chasmops* shows the shape, size, and distribution of the inner openings of the canals (Pl.32, fig. 6). Most of the circular openings have a diameter of 20 μm, but other sizes also occur in accordance with the size of the tubercles on the outer surface (Pl. 26, fig. 4*a*–*c*). Since the pit on the apex of the tubercle is much smaller than the inner opening, a widening of the canals is present in this type of tubercle. One section of a small tubercle of *C*. sp. nov. A (Pl. 28, fig. 5*a*, *b*) might represent two small pitted tubercles of the ordinary type with their thick internal canal. In the Devonian *Trimerocephalus caecus* the large tubercles have a prominent central canal reaching the surface (Osmolska 1975, pl. 1, figs. 2, 9; Pl. 31, figs. 6, 7). There are diverging fine canals around the central canal, features which might indicate a relationship with the composite tubercle in *Phacops*.

Cone type (text-fig. 1*e*). This relatively high and narrow tubercle is rarely preserved on exposed surfaces. The type has been studied in thin sections of *C. odini*, *C*. sp. nov. A, and *C*. sp. nov. D. In practically all sections of these three species the cones are truncated more or less at the same level. For this reason I was first inclined to regard the truncation as a primary feature with the apical 'crater' serving as a socket of a conspicuous seta. In *C*. sp. nov. A (Pl. 28, figs. 4*a*, *b*, 5*a*, *b*) the truncation is distinct, with a wide, partly pyrite filled, central canal opening at the top. However, in one case (Pl. 28, fig. 4*a*, *b*, right) a more complete cone is preserved. A similar condition is found in a young specimen probably of *C. odini* (Pl. 29, fig. 8). Here some of the cones have a smaller apical aperture which evidently is not due to rupture. Transitions between the cone type and the ordinary type of pit-tubercle can occur. The small tubercles with the powerful central canals shown on Plate 28, figure 6*a*, *b* are of this type.

In *C. odini* (Pl. 29, fig. 3) the truncate cone tubercle measures 70 μm in height and 120–125 μm in width. The diameter of the upper truncated surface or 'crater' is 6–7 μm. In *C*. sp. nov. A the corresponding dimensions of height and width are 45 μm and 95 μm, 70 μm and 100 μm, 90 μm and 100 μm, 80 μm and 90 μm (Pl. 28, figs. 4*a*–5*b*). In *C*. sp. nov. D the respective dimensions are 50 μm and 70 μm (Pl. 29, fig. 2). The secondary truncation at the summit represents a large aperture. This is demonstrated in one section of *C*. sp. nov. A (Pl. 28, fig. 4*a*, *b*, left) where the walls of the tubercle continue above the pyrite-filled central canal. A sac-like formation, light in crossed nicols, is present below the tubercle, and reaches about half the way down the section (Pl. 25, fig. 5*a*, *b*; Pl. 28, figs. 4*b*, 5*b*). Both the sac and the tubercle have indications of narrow lamellar layers forming a 'christmas tree structure'. The dimension of the laminated sac might indicate a relatively thick outer laminate zone. The large central canal penetrating the cone and the exoskeleton below is well shown in thin sections

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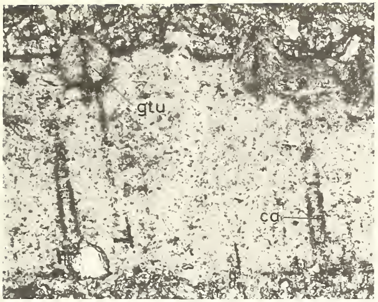
EXPLANATION OF PLATE 28

Figs. 1–3. *Toxochasmops extensus* subsp. nov. 1*a*, *b*, perpendicular; 1*c*, tangential sections of cephalic exoskeleton. Smooth tubercles of granule type. Tubercles pierced by fine central canal not continuing below onion-shaped body of tubercles. Wide canals evidently not opening through tubercles. 4bγ, Vestbråten, Røyse, Ringerike, PMO 68794, ×152.

Figs. 4, 5, 7. *Chasmops* sp. nov. A. 4*a*, *b*, exoskeleton of cephalon partly pyritized. Pit-tubercles of cone type broken off except to right; 4*b*, crossed nicols indicating dark inner (laminate) zone. 5*a*, *b*, broken cone tubercle and central canal. 7*a*, *b*, to show internal openings of central canal of tubercle. 4b, Østre brygge, Nesøya, Asker, PMO 94384, ×148.

Fig. 6. *Toxochasmops extensus extensus* (Boeck, 1838). Posterior portion of gena and pleura of first thoracic segment. Granulation lacking on the latter. 4bδ, Raudskjær, Asker, PMO 94412, ×90.

ca = canal, *gtu* = granule type of smooth tubercle, *th* = 1st thoracic segment.



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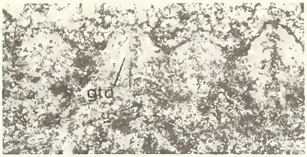

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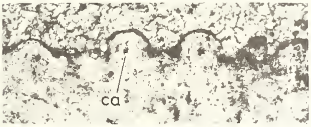

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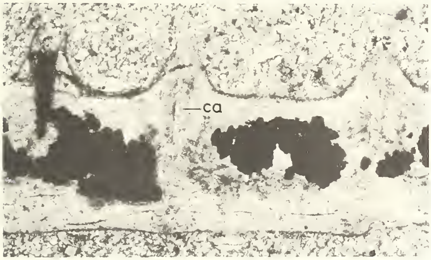

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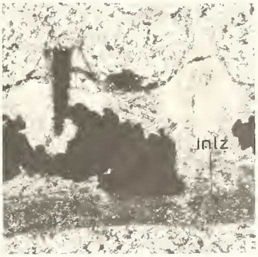

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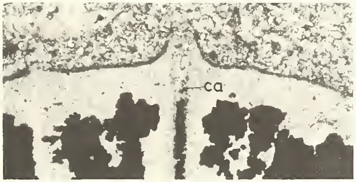

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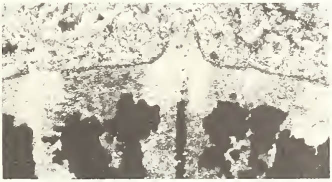

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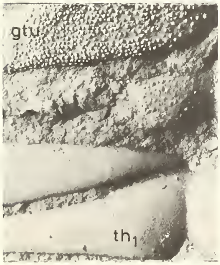

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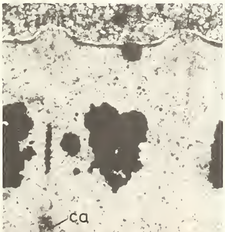

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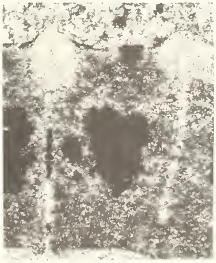

7b

STØRMER, trilobite sculpture

of *C. odini* (Pl. 29, fig. 3). The diameter of the canal within the tubercle is about 30 μm, and at the inner surface of the exoskeleton it flares to 75 μm. The inner openings are very distinct and narrowing upwards of the tunnel may be directly observed (Pl. 32, fig. 5; Pl. 33, fig. 3). In *C.* sp. nov. A the canals have similar dimensions.

Spine type (text-fig. 1*f*). Like the cone type, these thorn-like extensions would not be preserved on exposed surfaces. They are beautifully demonstrated, however, in silicified trilobites, e.g. in *Ceratocephala laciniata* described by Whittington and Evitt (1954, pl. 9, fig. 2). The spine tubercle is evidently rare among the Chasmopinae. Only in a thin section of *Chasmops* sp. nov. D a small spine tubercle occurs close to the eye (Pl. 29, fig. 1). The curved spine has a length of 60 μm and width at the base of 35 μm. A central canal is indicated.

Composite tubercles and internal tubular organ

These large, often discrete, pustules or mounds are probably formed by a fusion of separate tubercles. The separate small tubercles or elements in the specimens studied are either of the smooth granule type or of the ordinary type of pitted tubercles. Distinct composite tubercles have been figured by Dean (1961, pl. 52, fig. 6) in '*Chasmops*', and by Campbell (1977, pl. 7, fig. 2*b*) in *Paciphacops* (*Paciphacops*) *raymondi* (Delo).

Fused smooth tubercle type (text-fig. 1*g*). This type is well demonstrated in Norwegian species of *Toxochasmops* where the tubercular elements are of the granule type. In *Toxochasmops extensus extensus* the development of a composite tubercle from single-granule tubercles is shown on Plate 32, figure 9. We notice all transitions from a single tubercle, through a few fused tubercles, to a great number of close-set tubercles mounted on a dome. The dome has a characteristic shallow depression on the inner surface of the exoskeleton.

The fused pitted tubercle type (text-fig. 1*h*). A cast of a weathered specimen of *C.* sp. nov. A (Pl. 27, fig. 7) shows numerous pit-tubercles, most of them of the ordinary type. Some of the lobe-shaped smaller tubercles have several pits indicating simple composite tubercles formed by a fusion of a few pit-tubercles. A composite tubercle of this type would be difficult to distinguish in thin section where

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EXPLANATION OF PLATE 29

Figs. 1, 2. *Chasmops* sp. nov. D. 1, perpendicular section close to eye. Various tubercles and canals. To the right small spine type of pit-tubercle. 2, truncated cone tubercle, Osmolska cavities, and narrow outermost and innermost layer. Cyclocrinus beds (4bγ), Furuberget, Hamar District, PMO 21999, × 116.

Fig. 3. *Chasmops odini* (Eichwald, 1840). Large perpendicular canals flaring out towards the inner surface and opening on the outer surface through tubercles of cone type. C_2, Kukruse, Estonia. B.M. In. 5147/5 × 107.

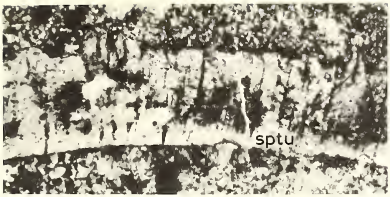
Figs. 4, 5. *Chasmops* sp. nov. B. Perpendicular sections through frontal lobe of glabella, A_1–A_2 in Pl. 26, fig. 1*a*. Outer laminate zone, which is mostly abraded, pierced by a very thin canal (fig. 4 right). 4bα(?), Tønnerud, Hadeland, PMO 57698, × 107.

Fig. 6. *Chasmops odini* (Eichwald, 1840). Perpendicular section across the anterior doublure of cephalon. 8-μm-wide canals through the exoskeleton. In the section of the doublure the upper part represents the inside of the exoskeleton. C_2, Kukruse, Estonia. B.M. In 5147/5, × 107.

Figs. 7*a*, *b*. '*Toxochasmops*' sp. Perpendicular sections through glabella showing traces of an outermost prismatic layer with Osmolska cavities just below. Each thin (1·5–2·0 μm) canal running upwards from the inner surface seems to be connected with one Osmolska cavity. Mjøsa limestone, 4bδ, Bergsvika, Helgøya, Hamar District, PMO 105704, × 183.

Fig. 8. ?*Chasmops odini* (Eichwald, 1840). Perpendicular section of glabella of young specimen; unbroken pit-tubercles of cone type well-preserved. C_2, Kukruse, Estonia. B.M. In 5147/5, × 107.

ctu = pit-tubercle of cone type, *ca* = canal, *sptu* = pit-tubercle of spine type, *ins* = inner surface, *ilz* = inner laminate zone, *prs* = prismatic layer, *osc* = Osmolska cavity, *oulz* = outer laminate zone.



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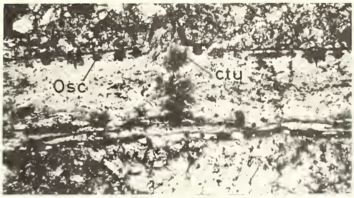

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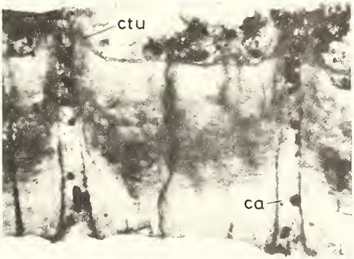

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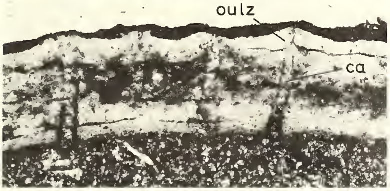

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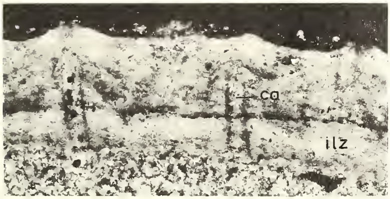

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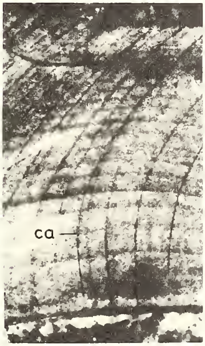

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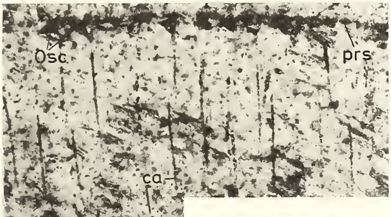

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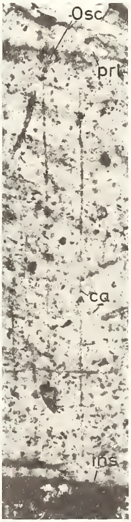

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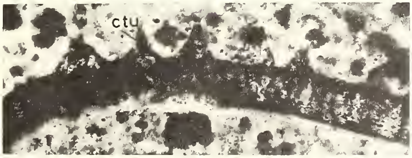


8

STØRMER, trilobite cuticle microstructure several canals rarely are sectioned in one plane. In *Toxochasmops* sp. nov. (Pl. 27, fig. 3*a*) the anterior portion of the glabella has separate pitted tubercles scattered on a finely granulated surface. Further back the surface is covered by clusters of tubercles forming composite tubercles (Pl. 27, fig. 3*b*, *c*). In another specimen (Pl. 27, fig. 4) the composite tubercles are less discrete but individual elements are clear.

Phacopid type (text-fig. 1*i*). Many authors have described the large globular tubercles on the glabella of various phacopid trilobites. In *Phacops rana africanus* Miller (1976) notices tubercles with diameters up to 2000 μm, while those described by Osmolska (1975) are about half that size, and in *Trimerocephalus caecus* the diameter ranges from 500 μm down to 160 μm. The last dimension is less than the diameter of 250 μm found in the smooth tubercles of *C.* sp. nov. B. In well-preserved specimens of *Phacops* the surface of the tubercles appears to be smooth, but Campbell (1967, p. 27) found seven to eight small perforations in a ring on the flanks, and Miller (1976, p. 351) mentions the presence of pits with a diameter of 20 μm. Vertical thin sections of composite tubercles in *Phacops* and *Trimerocephalus* have previously been figured by Dalingwater (1973), Osmolska (1975), and Miller (1976). The present specimens show several new structures in the outer portion of the exoskeleton. Plate 30, figures 1–8; Plate 31, figure 1*a*, *b*; text-figs. 3*a*–*d*, 5*a*–*e*, show the finer structures in normal and polarized light; SEM photographs are shown on Plate 34, figure 7*a*, *b*.

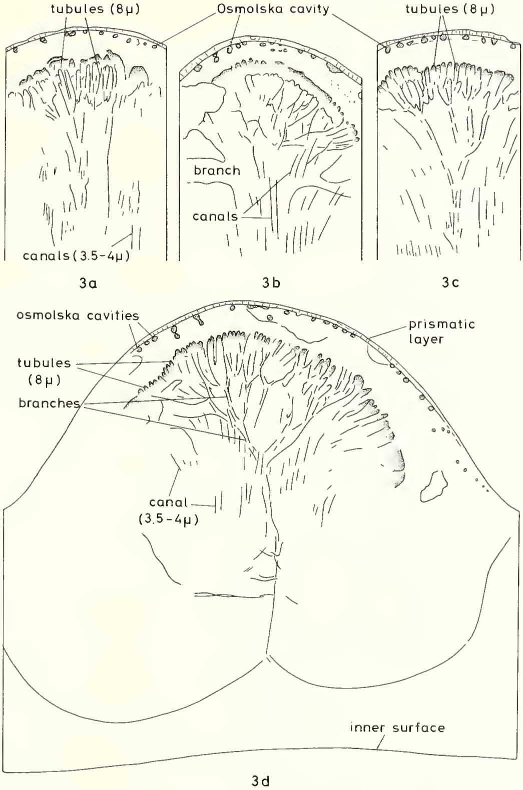
The convex tubercles have a height of about 300 μm and a width at the base of about 700 μm. In crossed nicols each tubercle has a light sac-like internal extension or halo divided in two halves by a dark vertical line (Pl. 30, figs. 1*a*–2*b*; text-fig. 4). In contrast to previously described specimens, ours show the outermost prismatic layer and the Osmolska cavities. Below the prismatic layer an outer, unlaminated, zone is distinguished by its lighter colour. The zone (including the layer with the Osmolska cavities) has a thickness of about 80–100 μm. The inner margin (Pl. 30, figs. 3*a*–7; Pl. 31, fig. 1*a*, *b*; text-fig. 3*a*–*d*) has numerous small notches or indentations with a diameter around 8 μm. The inner portion of the tubercle and the exoskeleton below are not divided into a central and inner zone. In crossed nicols (Pl. 30, figs. 1*b*, 2*b*) the darker inner portion below the 'light' sack or 'halo', might possibly have represented an inner zone, but since the darker colour also continues up to the outer surface between neighbouring tubercles, this seems less probable. In the SEM photographs, however, an inner, laminate zone is faintly suggested (Pl. 34, fig. 4).

In the tubercle and the exoskeleton below, the portion below the outer zone shows several different fine details:

Tubules with diameter about 8 μm. These cylindrical structures have blunt ends inserted into the notches at the inner surface of the outer zone. The direction of the straight tubules is normal to the surface. The closely packed tubules occur in vase-shaped bundles or 'bushes' which converge downwards into one unit or branch. The sections indicate that different bundles occur close behind each other so that the distal ends of the tubules cover more or less the whole internal surface of the outer zone. The dimensions of the bundles are largely the same which means that their bases are situated at about the same level. Assuming a fairly dense cover of tubules all over the outer surface of the inner portion of the tubercle, the number of tubules might have reached about 8000.

Diffuse internal branches. As mentioned above the tubules in each bundle unite at the base of the bundle forming one branch or stem. This is indicated in the specimens figured, although the branches are somewhat diffuse. Each branch apparently belongs to a system of bifurcating branches, as shown in the reconstruction (text-fig. 4). The bifurcation is indicated in crossed nicols particularly in one section (Pl. 31, fig. 1*b*; text-fig. 3*d*). A vertical section through the flank of one tubercle (Pl. 30, fig. 6; text-fig. 3*b*) shows traces of a broad basal stem from which a pair of thick horizontal bifurcating branches extend.

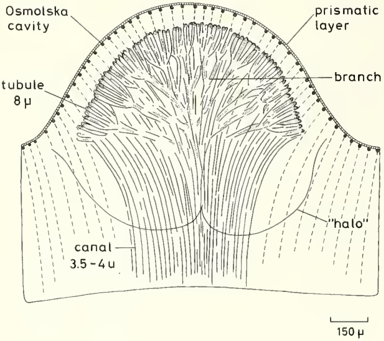
Distinct canals with a diameter of 3–4 μm. These densely packed canals are well shown in photographs taken by Osmolska (Pl. 31, fig. 5). Under high magnification each canal has a constant diameter. Below the tubercle the canals are vertical but at the base of the tubercle they spread fan-like towards the inner surface of the outer zone. The canals do not enter the outer zone. I have traced their courses upwards from the inner surface of the exoskeleton, but have not been able to trace their presence within the bundles of tubules. These canals have directions different from those of the branches described below. This is shown in the posterior portion of the



TEXT-FIG. 3. Perpendicular sections of composite tubercles in *Phacops granulatus* (Münster): *a* from Pl. 30, fig. 5, *b* from Pl. 30, fig. 6, *c* from Pl. 30, fig. 7, *d* from Pl. 30, fig. 3*a*, *b*; Pl. 31, fig. 1*a*, *b*, *b* with crossed nicols.

tubercles, where the canals are nearly vertical while the branches leading to the tubules are laterally directed (Pl. 30, figs. 1, 6; text-fig. 3*a*, *b*). Approaching the inner margin of the outer zone the tubules (8 μm) and the canals (3–4 μm) might have a common direction normal to the surface. The presence of the canals within the tubules have not been recognized.

Thus there are three different ducts penetrating the composite tubercle of the Phacopid type. In addition, a fourth type of duct or canal was evidently present leading to the Osmolska cavities, but except for certain very indistinct traces (Pl. 31, fig. 3) such canals have not been seen in the present material of *Phacops granulatus*. They appear to be present leading to the Osmolska cavities in



TEXT-FIG. 4. Reconstruction of composite tubercle in *Phacops granulatus* (Münster). The thin stippled canals from the Osmolska cavities are not demonstrated in the present specimens but suggested in *Toxochasmops* sp. (Pl. 29, fig. 7*a*, *b*).

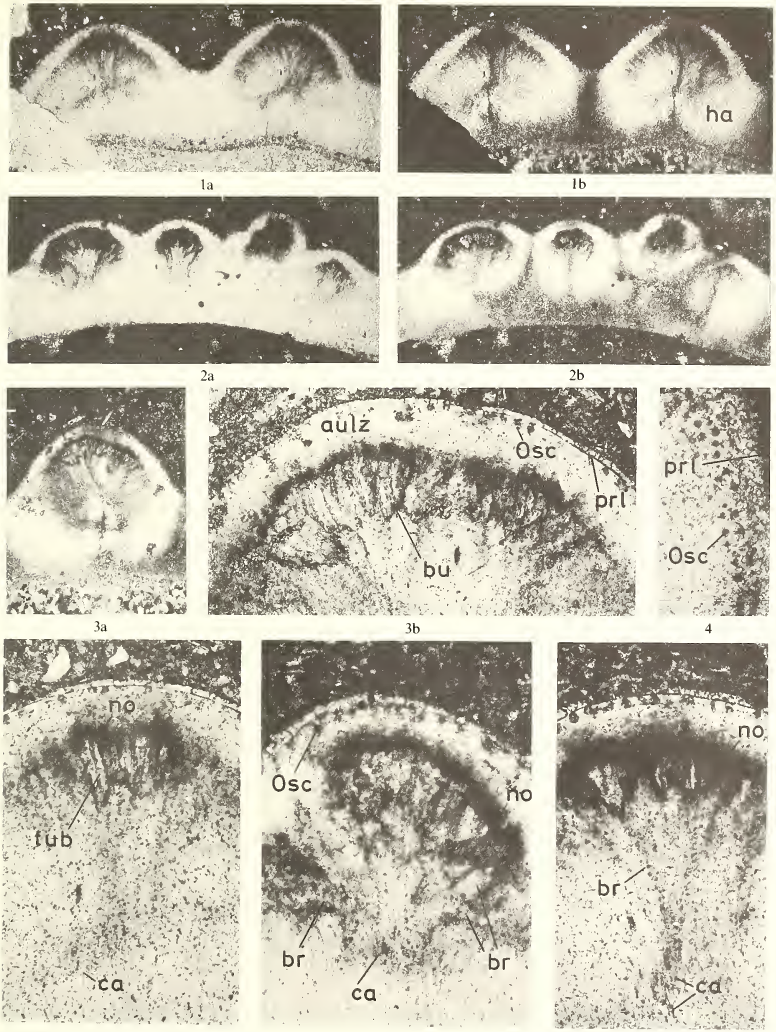
Toxochasmops (Pl. 29, fig. 7*a*, *b*). The very fine canals were not well preserved in the compact outer zone of the *Phacops* tubercle. In the reconstruction (text-fig. 4) the canals (1·5–2·0 μm) are indicated by stippled lines. While the 4-μm canals distinctly cross the directions of the proximal portions of the diffuse branches, the relations between the 4-μm canals and the 8-μm tubules are not clear. In two cases the canals are seen to abut to the bundles of tubules. The canals have not been traced up to the lower boundary of the outer zone; this might, however, be due to lack of preservation. So either the 4-μm canals pass into the wider tubules of the bundles, the increasing width of the tubules being due to an internal branching of the canals into closely packed microtubules similar to the microtubules in Diptera (text-fig. 7*f*); or the canals and tubules run independently up to the lower border of the outer zone. The first alternative seems the more probable.

These unique structures belong to some sensory organ or organs for which the term *internal tubules organ* is suggested. The function of the organ is discussed below.

EXPLANATION OF PLATE 30

Figs. 1–7. *Phacops granulatus* (Münster, 1840). 1*a*, 2*a*, perpendicular sections of composite tubercles of phacopid type on the glabella, ×40. 1*b*, 2*b*, the same in crossed nicols. 3*a*, *b*, tubercle in which the layer below the outer (laminate) zone is but slightly stained by iron oxide; 3*a* in crossed nicols indicates branching zone of tubules, ×40; 3*b*, upper part of tubercle with prismatic layer above Osmolska cavities in the upper part of the outer (laminate) zone. At the base of the zone notches for the terminals of tubules (8 μm) of the 'bush'-like bundles branching off at about the same level. Branches below the bundles faintly indicated below, ×100. 4, tangential section of tubercle showing Osmolska cavities and prismatic layer, ×100. 5, tubules (8 μm) with finer canals ((4 μm) below bundles of tubules, ×100. 6, perpendicular section through the flank of one tubercle. Traces of a diffuse broad stem with lateral branches. Fine canals crossing lateral branches, ×100. 7, section showing prismatic layer with Osmolska cavities, and the notches with the inserted dark terminals of tubules branching off at about the same level. The common basic branches below the bundles are indicated as 'shadows', ×100. Famennian of Poland.

br = branches below the bundles of tubules, *bu* = bundles of tubules, *ca* = canals (4 μm), *ha* = 'halo', light base of tubercle, *no* = notches marking terminations of tubules, *Osc* = Osmolska cavity, *oulz* = outer (laminate) zone, *prl* = prismatic layer, *tub* = tubule (8 μm).



1a 1b 2a 2b 3a 3b 4 5 6 7

STØRMER, *Phacops* tubercles

MICROSTRUCTURES NOT ASSOCIATED WITH LAMINATION AND TUBERCLES

These structures comprise the vertical canals not connected with sculptural elements on the cuticular surfaces, and the small cavities just below the outer surface of the exoskeleton. Structures associated with muscle attachments are described below.

Canals. Vertical canals penetrating the exoskeleton and opening directly on the flat outer surface are common in trilobites. The dimensions of the canals vary considerably. Osmolska (1975, p. 202) noticed two size groups, one with a diameter of less than 2μm and another with a diameter of 10–30 μm. Miller (1976, p. 349) distinguished three groups with diameters of 5–10 μm, 15–20 μm and 45–50 μm respectively. However, Dalingwater and Miller (1977, p. 29) proved that the narrowest canals were about 1 μm thick. Canals have recently been described by Campbell (1978). The present material comprises two main groups: fine, narrow canals up to 2 μm wide, and larger canals with variable sizes.

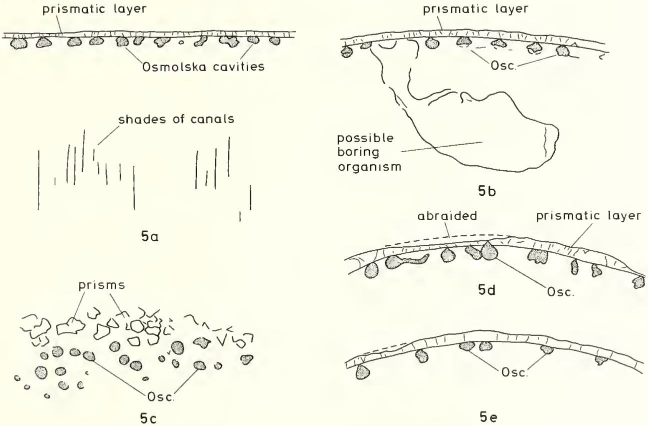
The narrow canals have recently been studied by Dalingwater and Miller (1977) who thought they could be compared with the pore canals of Recent arthropod cuticles. The minute canals have usually escaped preservation in our material. But beautifully preserved canals with a diameter of 1·5–2·0 μm are shown on *Toxochasmops* sp. from the Mjøsa Limestone (Pl. 29, fig. 7*a*, *b*; text-fig. 9*a*–*c*). Many of these are connected with the Osmolska cavities near the external surface. Similar narrow canals also occur in *Toxochasmops extensus extensus* (Pl. 32, fig. 2), and in *Chasmops* sp. nov. D (Pl. 29, fig. 1) which also shows larger canals. In *P. granulatus* the 4 μm canals seem to occur in the exoskeleton between the large tubercles (Pl. 34, figs. 3, 5, 6, 8). They are usually 3–4 μm wide, but in certain cases a corrosion or accretion of material seems to have taken place resulting in widths from 1·6–4·4 μm (Pl. 34, figs. 4, 5, 6). Near the surface a peculiar radiation of a bundle of vertical canals is present (Pl. 34, fig. 6). The canals in *Phacops* are normally limited to the central zone and parts of the inner zone (Pl. 34, fig. 3).

Wider canals occur in *C. odini*. In a section across the anterior doublure of the cephalon (Pl. 29, fig. 6) there are numerous curved canals, apparently with a diameter of about 8 μm. Larger canals opening directly on part of the upper surface are seen in *Chasmops* sp. nov. D, but thin sections near the eye show canals of a different width. On one side of the eye the canals vary considerably (Pl. 29, fig. 1). some of them connected with tubercles. On the other side (Pl. 32, figs. 1, 2) the canals have a fairly constant width of 10–20 μm. Some of the ducts are not perpendicular to the surface. These canals flare slightly on the inner surface, but not on the outer surface. Pits on the external surface representing openings of canals have been beautifully figured by Miller (1976, pl. 1, figs. 5, 6) in *P. rana*. Other pits have been demonstrated in *Tretaspis* by Størmer (1930, pl. 11, fig. 4*a*, *b*). In some of the *Phacops* specimens the pits measure 400 μm across, and form bowls containing up to five pits at the bottom.

Miller (1975, figs. 2A, 3F, 4D) interprets certain lines crossing the exoskeleton in trilobites as canals. The lines run inwards from the base of scarps along terrace lines. Similar lines have been described in sections of *Tretaspis* (Størmer 1930, p. 105) and in other trilobites (Kielan 1954, text-fig. 34). I described these lines from the terrace lines on the trinucleid fringe and from the reticulate ridge-pattern on the frontal lobe of the glabella, as 'stay lines'. Osmolska (1975, p. 204) observed that if they were canals one would expect to observe corresponding rows of evenly spaced pits or canal openings on the outer surface. Scanning electron micrographs (Miller 1975, fig. 4A–C) do not show such rows of canal openings. The many pits along the border (fig. 4C) would have shown a mixture of canals of different dimensions and mutual distances. I am still inclined to interpret the 'canals' as sections of some kind of laminae or sheets. It seems possible that the laminae, which have no observable thickness (Størmer 1930, p. 103), might mark the boundary between fine lamellae from the laminate zones, meeting at a distinct angle along the ridges.

Subsurface cavities and the Osmolska cavities. With the term 'external pitting' Osmolska (1975, p. 203, pl. 1, figs. 7–18) described very small and relatively shallow pits occurring in great numbers and more or less evenly distributed on the external surface of the integument in several Devonian trilobites. These structures had been previously figured by Dalingwater (1973, pl. 105, figs. 2, 3), and form tiny cavities measuring 12–15 μm in diameter and 10–18 μm in depth. The size seems to be rather constant, independent of the size of the individual. Miller (1976, p. 349, pl. 2, figs. 1, 6; text-fig. 2α) interpreted the 'external pitting' as 'artifacts' produced by tangential sectioning of the 20-μm-wide pits belonging to the 5–10-μm-duct group. An external pitting similar to that of the Devonian phacopids also occurs in *Chasmops* sp. nov. A (Pl. 25, fig. 3), *C.* sp. nov. D (Pl. 29, fig. 2), and *T. extensus extensus* (Pl. 25, fig. 2*a*, *b*).

Sections from some excellently preserved specimens of *P. granulatus* show details which necessitate a new concept of the 'external pitting'. As described above, the exoskeleton of the cephalon has an outermost prismatic layer about 10 μm thick (Pl. 30, figs. 3*b*, 5–7; Pl. 31, fig. 1*a*, *b*; text-figs. 3, 5, 6).



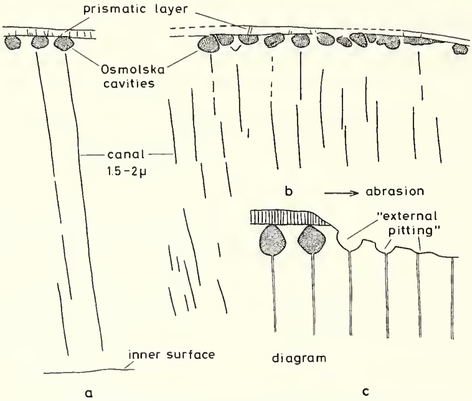
TEXT-FIG. 5. *Phacops granulatus* (Münster) from the Devonian of Poland. Prismatic layer with Osmolska cavity organs below: *a*, *b*, *d*, *e*, perpendicular sections of the glabella; *c*, tangential section. (*a* from Pl. 31, fig. 3; *b* from Pl. 31, fig. 3; *c* from Pl. 30, fig. 4; *d* from Pl. 30, fig. 7; *e* from Pl. 30, fig. 5).

The layer is partly worn off in some specimens, but not as much as in those figured by Dalingwater (1973, pl. 109, figs. 2, 3), Osmolska (1975, pl. 1, figs. 2–9, 11–20, reproduced on Pl. 31, fig. 5), and Miller (1976, pl. 2, figs. 1, 3, 4, 6). The present *Phacops* material shows that the external 'pits' are parts of cavities occurring distinctly *below* the prismatic layer. A small portion of the cavities may exceptionally invade the lowermost part of the prismatic layer (text-fig. 5*d*). Because of the numerous vertical lines forming the walls of the prisms (Pl. 34, figs. 1, 2) it is difficult to decide whether the cavities communicate with the outer surface. In vertical sections the cavities vary considerably from circular, flask- or pear-shaped to triangular (Pl. 31, fig. 4). In the last case the lowermost portion of the cavities evidently have not been filled with a fine brownish material, assumed to be iron oxide. The cavities extend downwards in the upper (laminate) zone to a level about 15–20 μm below the prismatic layer. In a few specimens this lower level or boundary is suggested by a faint line parallel to the surface (Pl. 30, fig. 7; Pl. 31, fig. 4). In tangential sections the cavities have a more or less circular outline with a diameter corresponding to the width in vertical sections (Pl. 30, fig. 4; text-fig. 5*c*). I propose the term *Osmolska cavities* for these structures.

SEM photographs do not pick out the colour contrast of the thin sections so that the Osmolska cavities are poorly displayed (Pl. 34, figs. 1, 2, 4, 7*a*, *b*). However, the position below the prismatic layer is evident. The width of the cavities varies from 10 to 20 μm.

In the cephalon of *Phacops* the distribution of the Osmolska cavities on the large tubercles is fairly regular as shown in the sections, limited areas without cavities might occur (Pl. 30, fig. 3*b*; text-fig. 3*d*). According to Osmolska (1975, p. 205) the cavities also occur on the doublure in *P. granulatus*. In sections of *Phacops* from areas without tubercles, Osmolska cavities may be very numerous (Pl. 31, fig. 3; text-fig. 5*a*). Closely packed cavities facilitate the breaking off of the prismatic layer in these specimens.

Structure apparently identical to the Osmolska cavities occur in three different Norwegian Chasmopinae a hundred million years older than the Fammenian occurrences in Poland. The Norwegian occurrences are sporadic, which may be due to imperfect preservation. When the cavities are absent so also is the prismatic layer. The absence of Osmolska cavities in most specimens might therefore be due to abrasion of the outermost cuticular layers of the exoskeleton (text-fig. 6*c*). In *Chasmops* sp. nov. A the pit-like structures are shown in the left part of the section. In *C.* sp. nov. D the round cavities are distinct (Pl. 29, fig. 2) and traces of a prismatic layer are visible to the right. Osmolska cavities are preserved in some thin sections of *T. extensus extensus* (Pl. 25, fig. 2*a*, *b*) and *Toxochasmops* sp. (Pl. 29, fig. 7*a*, *b*; text-fig. 6*a*, *b*). In the first species the cavities occur as pits between the granule tubercles and are lacking on the depressed surfaces interpreted as areas of genal muscle scars, in the second both cavities and traces of the prismatic layer are preserved. The cavities have a somewhat irregular outline, but the size is constant. Of particular interest is the presence of well-preserved thin (1·5–2·0 μm) vertical canals below the cavities. Some of the canals penetrating the exoskeleton seem to be directly connected with the Osmolska cavities near the external surface (Pl. 29, fig. 7*b*; text-fig. 6*a*, *b*).



TEXT-FIG. 6. *Toxochasmops* sp. from the Ordovician of the Hamar District. Prismatic layer with Osmolska cavity organs below: *a*, *b*, perpendicular sections showing the thin (1·5–2·0 μm) vertical canals probably connected with the Osmolska cavities above (Pl. 29, fig. 7*a*, *b*); *c*, reconstruction indicating several successive stages in the abrasion of the outermost part of the exoskeleton. The prismatic layer is removed, an 'external pitting' is formed, and finally, to the right, the outer surface appears as smooth.

The Osmolska cavities are either caused by boring organisms, or they are primary components of the exoskeleton. In favour of the first alternative is the fairly uniform size in various species and in young and adult specimens. Certain other structures in *P. granulatus* might indicate cavities formed by boring organisms, such as big sack-like structures of irregular outline (Pl. 31, figs. 2, 4). Teigler and Towe (1975, p. 139) have demonstrated the presence of a phosphatic layer near the surface of the exoskeleton in *Calymene*. If the Osmolska cavities were boring algae they might have preferred to live in a phosphatic layer near the surface. In *Phacops* there is apparently no phosphatic layer, because polished cuticular sections do not stain with MoO_2 and NH_3. In favour of the second alternative is lack of Osmolska cavities on the *lower* surface of the exoskeleton, their occurrence at a constant level below the outer surface and in distantly related trilobites from the Ordovician and the Devonian. Most important, however, is the presence of fine vertical canals evidently connecting the cavities with the epidermis below the cuticle. The arguments for their primary nature are more compelling, and the cavity probably housed a special organ.

POSSIBLE FUNCTIONS OF STRUCTURES DESCRIBED

The functions have to be deduced from a comparison with Recent arthropods, with the caution that similar structures, such as the composite eyes in crustaceans and insects, might develop independently in different groups. Analogous structures, however, might be an important key to the understanding of the functions of the organs in the fossil forms.

Pore canals, canals of sensory setae and of tegumental glands

The fine canals with a diameter below 1–2 μm have been interpreted by various authors as pore canals. The present material does not add new information of these tiny structures. It is probable that most of the finer and thicker canals through the exoskeleton in trilobites contained extensions of nerve cells in the epidermis. It is assumed that these extensions were connected with one or more hairs or sensory setae (sensillae) on the outer surface. (Dalingwater 1973, p. 837; Miller 1976, p. 345). The openings on the apex of the tubercles support this assumption. The actual movable setae, which easily break off, have never been observed in trilobites. Whittington and Evitt (1954, fig. 1) show the setae or hairs in their reconstruction of *Ceratocephala laciniata*. In the present material the pitted tubercles of various kinds probably carried setae on the apex. The thickness of the central canal and especially the apical aperture indicate the dimensions of the setae. Typical sockets with distinct surrounding ring or ridges like those in eurypterids and scorpions (Størmer 1963, text-fig. 45; pl. 12, fig. 1) have apparently not been observed in trilobites, and the only comparable structures are probably due to abrasion of tubercles (text-fig. 2).

The hair-like extensions and narrow spines occurring in *Triarthrus*, *Olenoides*, and *Ceraurus* (Raymond 1920; Størmer 1933; Whittington 1975) were probably fixed, not sensory extensions of the cuticle (macrotrichs of Weber 1954, p. 44). Probably the majority of cuticular setae in trilobites served as mechanoreceptors. In cases where the canals open into a large bowl-shaped pit on the surface, the setae would have had a considerable movability (not unlike the trichobotriae in Recent arachnids). In other cases a large bowl could have had a bundle of several setae. Major canals opening directly on a smooth surface might (Osmolska 1975, p. 202) have served as ducts for tegumental glands.

Smooth tubercle organ

The *campaniform organ* in Recent Crustacea and Hexapoda is compared with the smooth tubercle of *Chasmops*. In decapod crustaceans the organ (text-fig. 7*a*) consists of a canal around 8 μm wide penetrating the calcified exoskeleton and covered at the surface by a chitinous, relatively flexible, cap (Shelton and Laverack 1968). Inside the canal, extensions of two sensory neurones are united into a peg which touches the inside of the cap. Pressures on the cap are transferred to the epidermal neurones. In insects various developments of campaniform organs occur. One type (text-fig. 7*b*) resembles that of the crustaceans. A dome-shaped cuticular membrane has a peg underneath.

The low convex tubercle of the trilobites studied, has no discernable pit on the apex of the outer layer or 'cap'. Just below this layer, a wide vertical canal occurs which continues downwards to the lower surface of the exoskeleton (text-fig. 1*c*). The 'cap' and the canal, which narrows abruptly towards the 'cap', recall the structures of the campaniform organ in the Hexapoda. In that case the extensions of the neurones in the wide canal would have been united into a peg leading up to a 'cap' representing the outer zone of the exoskeleton. However, in contrast to the typical campaniform organ the smooth tubercle organ might have had a very thin canal penetrating the outer cap or layer.

Internal tubules organ

The composite tubercle of the phacopid type evidently had a special function. Miller (1976) points out the importance of the composite tubercle ('pseudotubercle') in *Phacops* as a sensory organ, and suggests that the tubercle served as some kind of a chemoreceptor. A special type of campaniform organ in Recent Hexapoda shows some similarity to the trilobite structures. In Diptera the halteres, which are modified second pairs of wings, have complex sensory organs serving as mechanoreceptors (Smith 1969; Grassé 1975). The very minute organs appear as convex papillae surrounded by a few hairs (Pl. 31, fig. 9). Perpendicular sections of a papilla (Pl. 31, fig. 8; text-fig. 7*d*–*f*) show: (1) a relatively thick and solid outer cap, (2) a thin and soft endocuticule with (3) a 'plasma membrane' (below a thin and dark inner thin cap) into which (4) numerous radially disposed narrow bundles of densely packed microtubules (0·01 μm) are inserted, (5) a reticulum of dark-walled lacunae occupying most of the prominent fan-like median portion, (6) discrete tubules with a diameter (0·02 μm), less than half that of the bundles, fill the space below the fan. In Diptera all the tubules and micro-tubules of one papilla belong to one epidermal cell only (Grassé 1975).

A comparison between the haltere-papilla and the phacopid composite tubercle shows the following resemblances and differences. In both cases the convex sensory tubercle or papilla has a relatively thick solid outer cap or zone, a dark endocuticule in the Diptera might possibly be compared with the dark-stained layers below the outer zone in *Phacops*. As in trilobites, the inner and basal portion of the papilla has numerous closely packed fine canals vertical at the base and spreading fan-like in the upper part. In both groups the terminals of tubules or bundles of microtubules, are inserted at the base of the external cap (into the soft 'plasma membrane' in Diptera). In the Diptera the tubules (with the microtubules inside) have a diameter about twice that of the canals below the fan-like portion of the organ. Also in *Phacops*, the tubules probably have about twice the width of the canals below the fan. On the other hand, the diameter of the tubercle is almost eighty times that of the papilla. The

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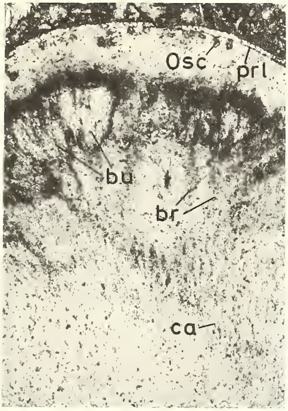
EXPLANATION OF PLATE 31

Figs. 1–5. *Phacops granulatus* (Münster, 1840). 1*a*, *b*, median portion of composite tubercle of phacopid type; 1*a* showing 'bush-like' bundles of tubules (8 μm) and canals (4 μm) at deeper levels; 1*b*, crossed nicols, the basal branching below the bundles is indicated. One diffuse stem runs down to the base of the exoskeleton, × 100. 2, oblique, nearly tangential section showing possible cavity of boring organism, × 100. 3, exoskeleton with prismatic layer and Osmolska cavities. Thin perpendicular canals are indicated, × 100. 4, details of prismatic layer and Osmolska cavities, large sac-like body possibly due to a boring organism, × 200. 5, 4-μm canals of tubercle of which portion below the outer zone is strongly stained, × 65 (after Osmolska 1975).

Figs. 6, 7. *Trimerocephalus caecus* (Gürich, 1840), Famennian Limestone, Poland. 6, tubercle with distinct layering and Osmolska cavities, × 95 (after Osmolska 1975). 7, perpendicular section of two pit-tubercles. Because of the indications of fine canals beside the central one this pit-tubercle might be related to the composite tubercle in *Phacops*. Osmolska cavities also present between the tubercles (after Osmolska 1975).

Figs. 8, 9. Sensory papillae (tubercles) of campaniform organ on halteres in Diptera. 8, perpendicular section of papilla with structures compared with those in *Phacops*, × *c*. 15 000. 9, papillae (tubercles) with setae in between, × 2000 (after Smith 1969).

bbt = basal branch below bundles of tubules, *bu* = bundle of tubules, *cbo* = possible cavity of boring organism, *ca* = canal, *Osc* = Osmolska cavity, *prl* = prismatic layer, *tub* = tubule.



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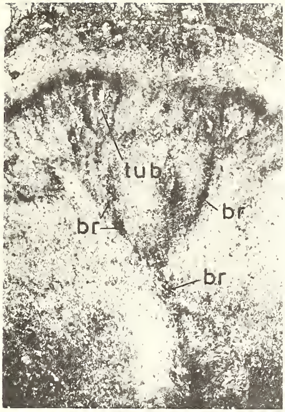

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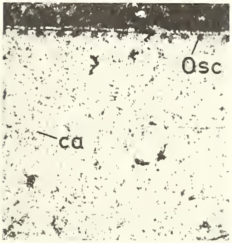

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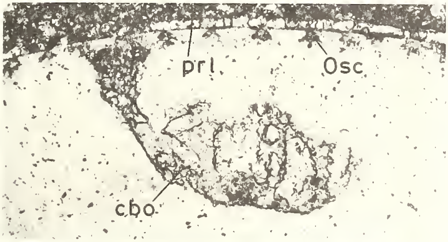

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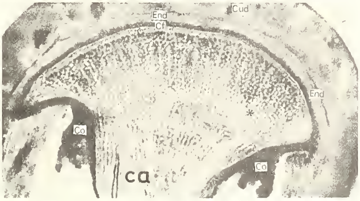

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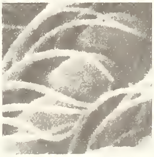

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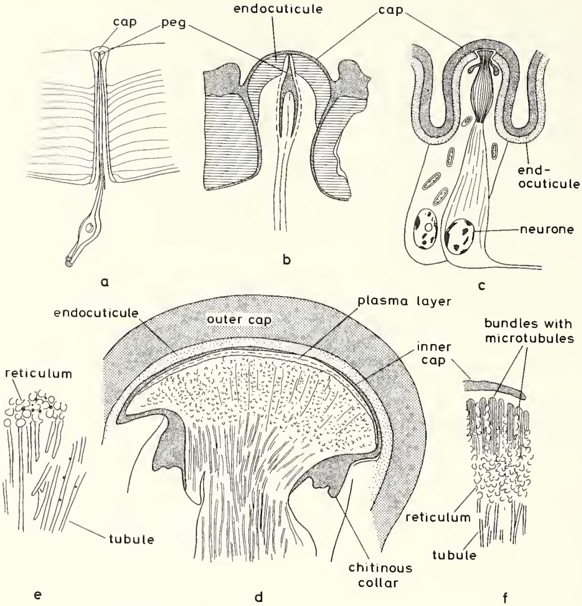
STØRMER, trilobite tubercle structure



TEXT-FIG. 7. Sensory campaniform organs in Recent arthropods: *a*, decapod crustacean (after Shelton and Laverack 1968); *b*, more simple organ in Hexapoda (after Grassé, 1975); *c*, composite organ in a haltere of Diptera (after Grassé, 1975 from Snodgrass); *d*, perpendicular section of papilla of a campaniform organ in a haltere of Diptera, corresponds to upper part of fig. 7*c*; *e*, detail of tubules; *f*, details of tubules with reticulum and microtubules (after Smith 1969).

papilla lacks the outermost prismatic layer and Osmolska cavity organ, and there is no trace of the branches with the distal bundles of tubules as in the tubercle of *Phacops*. The preservation of the trilobite tubules does not show microtubules within them. The position of the sensory tubercles and papillae is obviously also very different in the two groups.

The similarities are probably enough to suggest that the tubules in trilobites might have registered variations in water pressure, in a way analogous with the particular campaniform sensory organ in insects which records changes in air pressure.

Osmolska cavity organ

I have not been able to find any discription of a similar organ in Recent arthropods. If the big tubercles in *Phacops* served as a mechanoreceptor, the Osmolska cavity organ possibly had another function. It has not been possible to decide whether or not the cavities, situated just below the prismatic layer, had access to the surrounding water environment through one or several fine ducts. If an access was present, a chemoreceptor function might have been possible.

MUSCLE INSERTION AREAS

In *Chasmops* and Phacopidae smooth, outer exoskeletal surfaces are confined to particular areas: the axial and pleural furrows of thorax and pygidium, and the furrows of the cephalon. The smooth areas usually correspond to processes on the inner surface which served as apodemes for muscle attachment. Eldredge distinguishes four main types of areas of muscle attachment: (1) exoskeletal invaginations, (2) calluses or pads, (3) dark markings, and (4) pits or scars. Below it is shown that absence of canals through the exoskeleton is also characteristic of areas of muscle attachments or muscle scars. The familiar major invaginations serving as apodemes on the inner surface are not described here; we describe muscle attachments on and within the exoskeleton of the glabella and genae in the Chasmopinae.

Glabellar muscle scars (*auxiliary pits*)

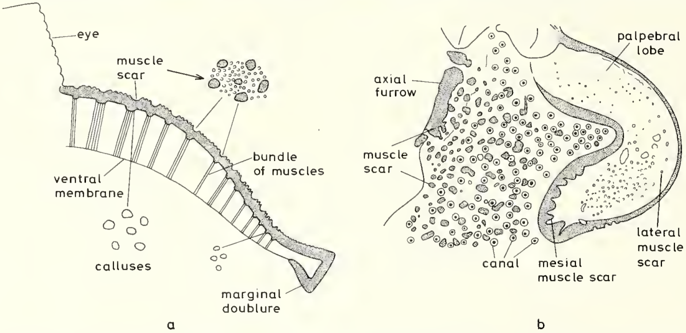
Barrande observed what he called 'impressions auxiliaires' on the frontal lobe of the glabella in phacopids. Born (1919) described these structures in *Chasmops odini*, and more recently Eldredge (1971) has reviewed the previous literature. He figured auxiliary impressions in many different genera of the Phacopidae. In the Chasmopinae a typical 'necklace' arrangement of the muscle scars occurs.

In specimens of *T. extensus extensus* and *T. extensus* subsp. nov. both the scars on the outer (Pl. 27, figs. 2*b*, 5; Pl. 32, figs. 7, 10) and inner (Pl. 27, fig. 3; Pl. 32, fig. 8) surface of the exoskeleton can be seen. On the outer surface each scar forms a small depressed smooth area or shallow pit surrounded by small smooth tubercles of the granule type. The granules are to some extent radially arranged round the depressed area. In *Toxochasmops* sp. nov. the anterior pairs of scars form small pits (Pl. 27, fig. 3*a*). The area varies in outline from circular to oblong. On the *inner* surface the areas of muscle attachment appear as low, flat calluses or pads. The two scars in the preglabellar furrow are more prominent than those behind. The shape and distribution of individual scars are highly variable. A triangle of three major scars may occur behind the single row of scars (Pl. 26, fig. 2*a*; Pl. 32, fig. 8). *C. odini* (Pl. 32, fig. 5) shows a V-shaped row of dark calluses or pads on the inside of the exoskeleton. One extra callus or muscle scar occurs in the middle and in the left row, one callus is double. The dark colour of the calluses is characteristic of muscle scars in well-preserved trilobites. The figured specimen also shows the openings of major canals connected with pit-tubercles, probably of the cone type, on the outer surface of the exoskeleton. None of the calluses or pads are penetrated by a canal, a condition which confirms their function as muscle scars. A canal containing an extension of a cell in the epidermis would hardly occur among muscle fibrils attached to the muscle scars or apodemes. The same lack of canals is noticed on the internal mould of *Chasmops* sp. nov. C (Pl. 32, fig. 6; text-fig. 7). In *Chasmops* sp. nov. B (Pl. 26, fig. 1*a*; Pl. 32, fig. 4) the muscle scars appear on the dorsal surface as deeper pits rather than shallow depressions. In the preglabellar furrow two small pits are seen between the larger ones.

The functions of the muscle scars related to the anterior portion of the digestive tract seems reasonable. The prominent scars in the preglabellar furrow and the three markings behind the 'necklace' might have served other purposes. Campbell (1977, fig. 26*b*, *c*) interprets muscle scars on the anterior portion of the frontal glabellar lobe as belonging to muscles leading to a presumed anterior ventral cephalic bar.

Genal muscle scars

Within the order Phacopida the surface of the cheeks is provided with both tubercles and pits. This kind of sculpture differs in related species (*Placoparia*, Henry and Clarkson 1975, text-fig. 3). In *C. odini* the granulated outer surface has certain pits and smooth depressed circular areas (Pl. 33, fig. 4) resembling the glabellar muscle scars in *T. extensus extensus* (Pl. 32, figs. 7, 10). On the inside of the exoskeleton in *C. odini* numerous dark calluses or pads occur, diminishing in size towards the marginal rims above the doublure, where they are absent (Pl. 32, fig. 11; text-fig. 8*b*). Adaxial to the palpebral lobe the inner surface of the genal exoskeleton shows numerous dark markings between openings of major canals identical to those on the inner surface of the glabella (Pl. 33, fig. 3; text-fig. 8*b*). The dark colour of the markings suggests the presence of small muscle scars. This interpretation is confirmed by the fact that the scars are not penetrated by the canals. Other Baltic species with their white exoskeletons, e.g. *Ceraurus aculeatus* (Öpik 1937, pl. 18) also have small dark scars partly mounted on calluses, on the inside of the genae. They also alternate with pits representing



TEXT-FIG. 8. Probable genal muscle scars in *Chasmops odini* (Eichwald): *a*, diagrammatic section of lateral portion of gena with details of outer and inner surfaces of exoskeleton; *b*, inside of exoskeleton of portion of gena and palpebral lobe showing canals and muscle scars.

EXPLANATION OF PLATE 32

Figs. 1, 2. *Chasmops* sp. nov. D. Exoskeleton (close to eye) devoid of tubercles but pierced by major canals. Cyclocrinus beds, 4bγ, Furuberget, Hamar District, PMO 21999, ×112.

Fig. 3. *Toxochasmops extensus* (Boeck, 1838). Perpendicular section through glabella. Osmolska cavities and fine canals. 4bδ, Rauskjær, Asker, PMO 94401, ×100.

Fig. 4. *Chasmops* sp. nov. B. Glabellar muscle scars between smooth tubercles of convex type on anterior portion of frontal lobe of glabella. To the right upper layer of tubercles partly abraded. 4bβ, Ostøya, Asker, PMO 20396, ×8·2.

Fig. 5. *Chasmops odini* (Eichwald, 1840). Inner surface of exoskeleton of frontal lobe with glabellar muscle scars appearing as a somewhat asymmetric row of calluses. Calluses devoid of canal openings. C_2, Kukruse, Estonia, RMS Ar. 46034, ×8·2.

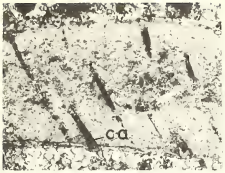
Fig. 6. *Chasmops* sp. nov. C. Anteromedian portion of glabella of internal mould. Glabellar muscle scars devoid of canal openings. In pre-glabellar furrow, larger pits with smaller pits between. 4bα, Bratterud, Røyse, Ringerike, PMO 69395, ×8·2.

Fig. 7. *Toxochasmops extensus* subsp. nov. Glabellar muscle scars on the outer surface of the exoskeleton appearing as shallow depressions devoid of the surrounding smooth tubercles of granule type. 4bγ, Vestbråten, Røyse, Ringerike, PMO 69345, ×12.

Figs. 8–10. *Toxochasmops extensus extensus* (Boeck, 1838). 8, inner surface of anteromedian portion of the glabellar exoskeleton. Narrow 'necklace' with three extra muscle scars behind. Two larger muscle scars in pre-glabellar furrow. 4bδ, Gåsøy, Bærum, PMO 63592, ×9. 9, details of anterior portion of glabella demonstrating an increasing density of smooth tubercles of the granule type resulting in the formtion of a composite tubercle, PMO 94412, ×28. 10, two auxiliary pits surrounded by granule tubercles partly radially arranged, ×28, as Fig. 9, Rauskjær, Asker.

Fig. 11. *Chasmops odini* (Eichwald, 1840). Lateral portion of gena with calluses forming muscle scars decreasing in size towards the lateral border. C_2, Kukruse, Estonia, RMS Ar. 46033, ×9.

ca = canal, *cal* = callus or pad, *cao* = canal opening or its impression, *eyf* = eye furrow, *Osc* = Osmolska cavities.



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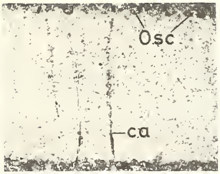

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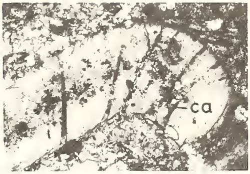

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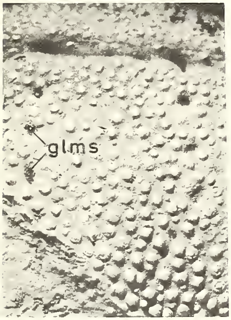

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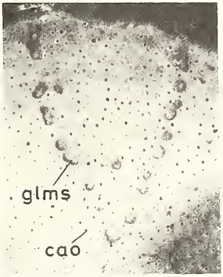

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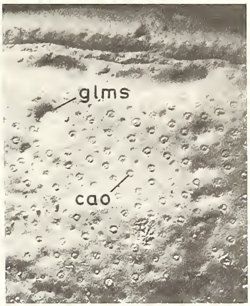

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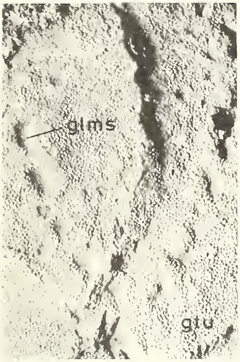

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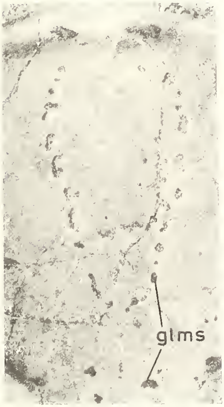

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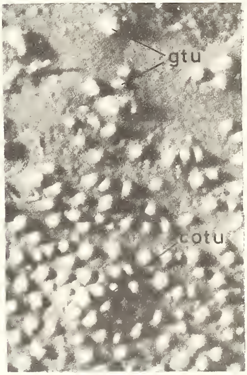

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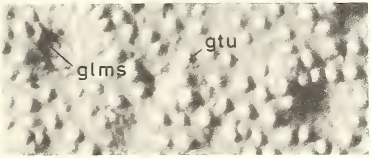

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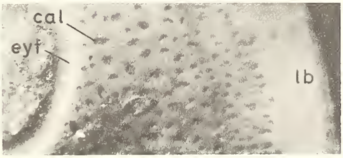


11

STØRMER, Chasmopinid cuticle structure

canal openings. We have made similar observations on *Chasmops* sp. nov. D (Pl. 33, fig. 1) and *Toxochasmops extensus* (Pl. 33, fig. 2). In another specimen (Pl. 32, fig. 8) the adaxial portion of the gena has dark markings like those in *C. odini.*

A thin section across the gena close to the eye of a specimen of *T. extensus extensus* shows interesting details of the shallow depressions on the external surface (Pl. 25, fig. 2*a*, *b*). The smooth surface of the depressions are surrounded by a surface provided with tubercles of the granule type and with the lower part of Osmolska cavities. The prismatic layer is evidently abraded. Of particular interest is the dark colour of the exoskeleton below the depressions. The dark colour, evidently due to fine-grained pyrite, might have been caused by decomposition of organic matter in the exoskeleton. In Recent arthropods the muscles are attached by tonofibrils, and Weber (1954, p. 57, figs. 23, 31) notes that the new cuticle formed after moulting might develop so rapidly that the tonofibrillar attachment can remain as a visible cone ('Faserkegel') within the exoskeleton. The dark colour in the specimen figured (Pl. 25, fig. 2*a*, *b*) might be interpreted as due to a decomposition of tonofibril substance formed during the growth of the exoskeleton after moulting.

Thus chasmopids probably had many narrow bundles of genal muscles with a dorso-ventral vertical direction. These were probably attached either to the genal caeca or to the ventral integument of the gena, which needed support by numerous bundles of muscles (text-fig. 8*a*). This was not the case with the thick and solid marginal doublure where there are no signs of muscle insertion. If the muscles reached the ventral cuticle they had to pass strongly ramified caeca, probably of the kind known in *Elyx* and *Ptychoparia* (Harrington 1959, fig. 73).

Additional muscle scars are indicated by a darker colour in *C. odini* (Pl. 33, fig. 3). The palpebral lobe has a row of small scars near the lateral border. Similar structures have been figured by Clarkson (1975, pl. 6, fig. 8) in *Reedops*. Muscle scars also occur on the median (adaxial) margin of the palpebral lobe. The nature of these scars are unknown.

SUMMARY

The trilobite exoskeleton includes an outer, prismatic layer, and inner laminate layers with varied development. The external surface of the exoskeleton has a characteristic sculpture—tubercles of various kinds. Three main groups of tubercles are recognized: smooth tubercles, pitted tubercles, and composite tubercles. In the small granule type of smooth tubercles a central canal is observed as a very thin duct in the upper part of the exoskeleton. The medium-sized, low, convex smooth tubercle has (below the outer zone) a wide, perpendicular canal which might continue upwards through the outer zone as a very thin duct or canal. This kind of tubercle can be compared with the sensory campaniform organs in Recent arthropods. Wide openings in tubercles are interpreted as due to abrasion. Pitted tubercles have a distinct central canal with an apical aperture.

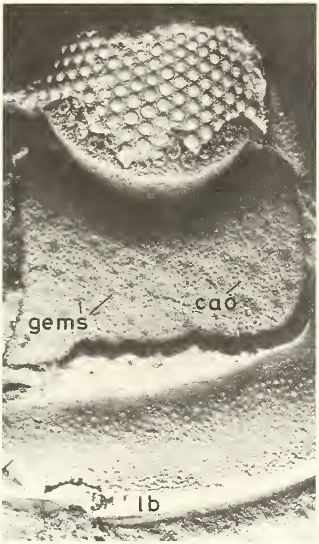
EXPLANATION OF PLATE 33

Fig. 1. *Chasmops* sp. nov. D. Lateral view of eye with internal mould of librigena and outer surface of lateral border. On the internal mould genal muscle scars and numerous impressions of canal openings. Cyclocrinus beds (4bγ) Røykenvik, Hadeland, PMO 34109, × 11.

Fig. 2. *Toxochasmops extensus extensus* (Boeck, 1838). Dorsolateral view of eye and gena with crossing facial suture. Outer surface with granule tubercles, internal mould with genal muscle scars forming pits corresponding to calluses on inner surface. 4bδ, Bjerkøy, Asker, PMO 94322, × 11.

Figs. 3, 4. *Chasmops odini* (Eichwald, 1840). 3, inner surface of gena with palpebral lobe and part of glabella. Dark circular canal openings surrounded by narrow light rims. Dark spots, not penetrated by canals represent genal muscle scars. Special muscle scars also on palpebral lobe. C_2, Kukruse, Kiviöti, Estonia. B.M. In 51475, × 12·9. 4, details of outer surface of gena near occipital furrow. Circular muscle scars forming smooth depressions between close-set small tubercles, some with central pits. B.M. In 51475, × 40.

cao = canal opening or its impression, *fs* = facial suture, *gl* = glabella, *gems* = genal muscle scar, *gtu* = granule type of smooth tubercle, *ib* = lateral border, *ms* = muscle scar, *pal* = palpebral lobe.



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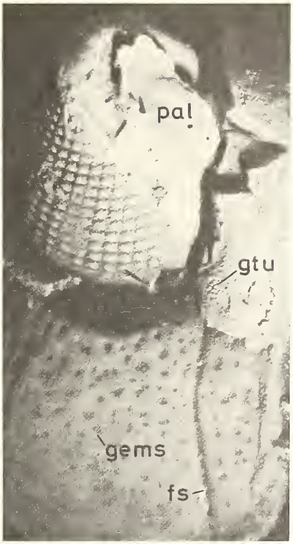

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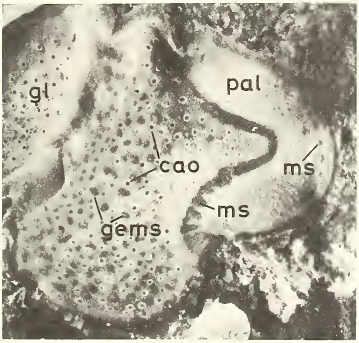

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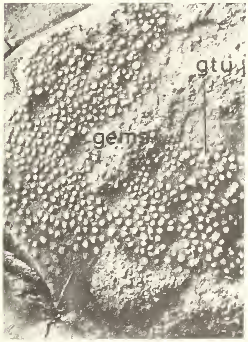

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STØRMER, Chasmopinid cuticle structure

Three types of composite tubercles occur, two formed by fusion of small smooth tubercles or pitted tubercles respectively, and the complex type occurring in Devonian Phacopidae. The phacopid convex composite tubercle has a thin (8–10 μm thick) outermost prismatic layer, a thin (10–20 μm) layer with small (15–20 μm wide) Osmolska cavities forming the upper part of a thicker (80 μm) unlaminated light outer zone. This zone apparently has close-set basal notches into which about 8-μm-wide tubules, ascending from the central zone, are inserted (text-fig. 4). In the dark-stained outer part of the central zone the tubules are arranged in bush-like bundles branching off more or less at a common level from diffuse bifurcating branches. Apparently independent of these structures the whole interior of the tubercle is filled by densely packed 3–4 μm canals, vertical in the lower part and spreading fan-like upwards towards the outer light zone. The canals partly cross the diffuse branches, it is uncertain, however, whether the canals are connected with the tubules in the bush-like bundles. *Phacops* tubercles have several features in common with the much smaller campaniform organ in the halters of Recent Diptera, an organ serving as a mechanoreceptor.

Apparent external pitting of the exoskeleton is shown to be due to abrasion of small round cavities occurring in considerable numbers in a layer just below the rarely preserved prismatic layer. The cavities, the Osmolska cavities, occur both in Devonian *Phacops* and in Ordovician Chasmopinae. In the latter very thin (1·5–2·0 μm) vertical canals seem to be connected with the cavities.

Canals not associated with tubercles on the surface are of several kinds. Thin canals with a diameter up to 2 μm might correspond to pore canals. Certain vertical lines seen in section crossing the exoskeleton are interpreted as subvertical laminae rather than true canals.

Glabellar muscle scars are not penetrated by canals, and the same is the case with the numerous small markings on the outer and inner surface of the exoskeleton of the genae in well-preserved specimens. These structures are interpreted as due to narrow bundles of muscle supporting the thin ventral integument inside the marginal doublure. Necklace-like muscle scars on the glabella of chasmopinids were mostly related to muscles attached to the anterior part of the intestinal tract.

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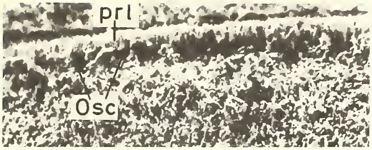
EXPLANATION OF PLATE 34

Figs. 1–8. *Phacops granulatus* (Münster, 1840), Devonian Famennian Limestone of Poland. 1, prismatic layer at the surface with traces of Osmolska cavities below, × 300. 2, prismatic layer, × 1000. 3, section through the exoskeleton with Osmolska cavities and canals. An outer zone is faintly indicated, × 150. 4, section through the exoskeleton with Osmolska cavities below a prismatic layer. An outer (laminate) zone with traces of parabolic structures either primary, or due to imprints of rhombic calcite crystals, × 200. 5, details of corroded perpendicular canals, × 500. 6, small cone-shaped protuberance (tubercle?) within which a star-like radiating arrangement of canals is suggested. From this 'star' a bundle of perpendicular canals extend downward as far as to the inner zone, × 150. 7*a*, *b*, composite tubercle near the eye. Prismatic layer preserved to the left, abraded to the right. Osmolska cavities present below the prismatic layer. Tubules and canals not distinguished but a possible branching zone of the former is suggested, *a*, × 150, *b*, × 300. 8, parts of perpendicular canals with a diameter of 4 μm, × 400.

br = diverging branches (?), *ca* = canal, *im* = inner margin, *ilz* = inner laminate zone, *osc* = Osmolska cavity, *oulz* = outer laminate zone, *prl* = prismatic layer.



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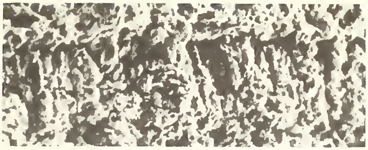

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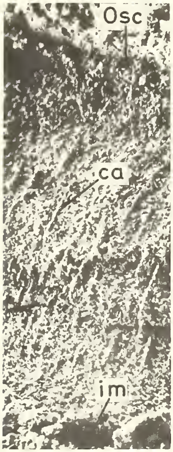

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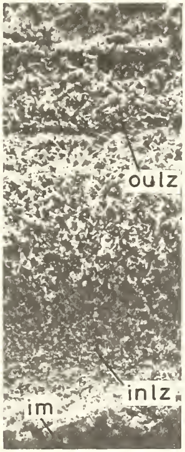

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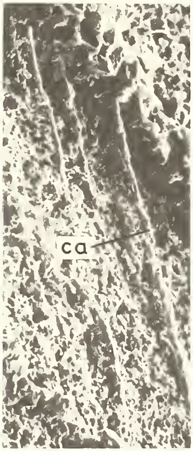

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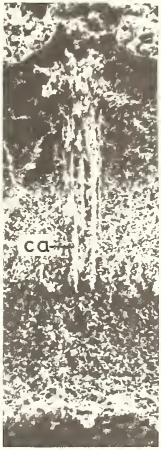

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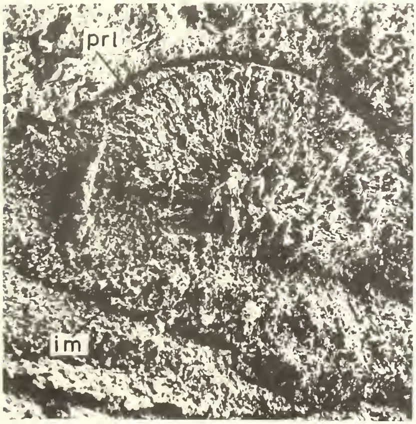

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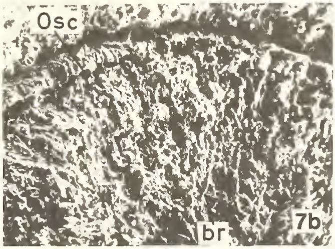

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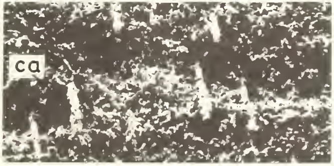

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STØRMER, *Phacops* cuticle structure

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THE AXIAL SKELETON OF THE CARBONIFEROUS AMPHIBIAN *PTEROPLAX CORNUTUS*

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ABSTRACT. The vertebrae and ribs of the Carboniferous amphibian *Pteroplax cornutus* Hancock and Atthey, 1868 are described. The vertebrae are embolomerous and in most respects similar to those of the much-larger embolomere *Eogyrinus attheyi* Watson, 1926. *Pteroplax* vertebrae differ from those of *Eogyrinus* in possessing intercentra which are as thick dorsally as ventrally and in the presence of a supraneural canal in at least the anterior trunk vertebrae. The supraneural canal may have housed a longitudinal ligament serving to strengthen an elongate presacral vertebral column. The trunk centra of sub-adult individuals exhibit large notochordal foramina, and the intercentra lack a ventro-lateral covering of periosteal bone. The precocious development of the lateral boss in such juvenile intercentra suggests that this structure, rather than the depression ventral to it in the fully formed centrum, formed the site of the capitular articulation.

PTEROPLAX CORNUTUS Hancock and Atthey, 1868 is a medium-sized anthracosaur amphibian of the infra-order Embolomeri from the Coal Measures of Great Britain. The type material of the species, stored in the Hancock Museum, Newcastle upon Tyne, is from the black shale immediately overlying the Low Main Seam at Newsham in Northumberland. This horizon lies within the Upper *Modiolaris* zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age in European terminology. The lectotype specimen, so designated by Romer (1963), consists of a well-preserved skull table in association with two trunk ribs. The lectotype skull table was first described by Hancock and Atthey (1868) and was redescribed and figured in great detail by Atthey (1877). The taxonomy and relationships of *Pteroplax* have recently been discussed by Panchen (1970, 1972).

Despite being one of the first Carboniferous amphibians to be described, *Pteroplax cornutus* has, by reason of the paucity of described material, remained poorly known. Although numerous isolated skull and postcranial elements were referred to this species by Hancock and Atthey (1868) and Atthey (1877), almost all have since proved to belong to other species of amphibian and crossopterygian fish (e.g. Watson 1926; Andrews 1972; Boyd 1978). Of the specimens originally attributed to *Pteroplax* by Hancock and Atthey, only the vertebrae and ribs noted by Atthey (1877, p. 374) appear to belong to this form. Amongst the amphibian specimens from Newsham in the collections of the Hancock Museum, however, are a number of further specimens of embolomerous vertebrae and ribs, listed below, which are in this present study attributed to *Pteroplax*.

Although no vertebrae are preserved in association with the lectotype skull table of *Pteroplax*, there is little doubt that the attributed axial skeletal elements do pertain to this form. The large numbers of embolomerous vertebrae from Newsham fall into two distinct size ranges. Many of those in the larger category, having centra mostly ranging between 38 and 48 mm in diameter, have been described as belonging to the large eogyrinid *Eogyrinus attheyi* Watson (Watson 1926; Panchen 1966), the only embolomere other than *Pteroplax* which is known to occur at Newsham. A series of vertebrae of this size are, indeed, preserved with the lectotype skull of *E. attheyi* (Panchen 1972). The embolomerous vertebrae which comprise the smaller size group possess centra of between 21 and 26 mm in diameter. Reference of these vertebrae to *Pteroplax* is clearly justifiable on the principle of parsimony of hypotheses, and the dimensions of the lectotype *Pteroplax* skull table, which is markedly narrower than that of *Eogyrinus* (Atthey 1877; Panchen 1972), are in accordance with such

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an attribution. Somewhat more positive evidence is afforded by the close similarity in size and morphology between the two ribs associated with the *Pteroplax* lectotype and those preserved with the vertebrae attributed to this form. It is of interest, also, to note Atthey's (1877) statement that the vertebrae which comprise Hancock Museum specimen G83.68 were collected from 'the same part of the mine' as the lectotype skull table of *Pteroplax*.

Although an account of the axial skeleton of the large embolomere *E. attheyi*, contemporary and sympatric with *Pteroplax*, has been given by Panchen (1966), no detailed description has hitherto been published of the vertebrae and ribs of a member of the smaller of the two embolomere size groups noted by Romer (1963). *P. cornutus* falls within the smaller of Romer's embolomere size groups and this, together with the fact that its vertebrae differ from those of *Eogyrinus* in several points of structure, would appear sufficient to justify detailed description of the axial skeleton, so far as known, of this species.

MATERIALS AND METHODS

All the specimens employed in the present study are from the black shale overlying the Low Main Seam at Newsham, Northumberland, and are stored in the Hancock Museum in Newcastle upon Tyne. A complete list of specimens used, with their Hancock Museum registration numbers, is as follows. G4.83, caudal intercentrum with haemal arch; G15.73, seven articulated trunk vertebrae in association with four ribs (cited and referred to *Megalocephalus pachycephalus* (as '*Loxomma*') by Hancock and Atthey 1870); G15.76, (?*Pteroplax*), presacral rib from mid-trunk region; G15.77, (?*Pteroplax*), posterior trunk rib; G15.78, (?*Pteroplax*), presacral rib from mid-trunk region; G15.80, (?*Pteroplax*), posterior trunk rib; G83.68, trunk pleurocentrum, intercentrum, and one indeterminable central element in association with two neural arches and three ribs (referred to *Pteroplax* by Atthey (1877) but not figured by this author); G83.69, two trunk pleurocentra, two intercentra, and fragments of five ribs; G83.72, (?*Pteroplax*), rib from posterior region of trunk; G83.73, (?*Pteroplax*), rib from (?)pectoral region of trunk; G83.74, (?*Pteroplax*), posterior trunk rib; G86.61, caudal intercentrum with haemal arch.

Preparation of specimens has been accomplished by the use of an S. S. White Industrial Airbrasive Unit (Stucker 1961), employing sodium bicarbonate as the abrasive powder. When necessary this procedure was supplemented by the use of mounted needles. A dilute solution of 'Perspex' in chloroform was applied to reinforce areas of friable or damaged bone surface and a more concentrated solution was used in the mending of broken fragments.

TRUNK VERTEBRAE

Three specimens, each including a number of trunk vertebrae, are available for study.

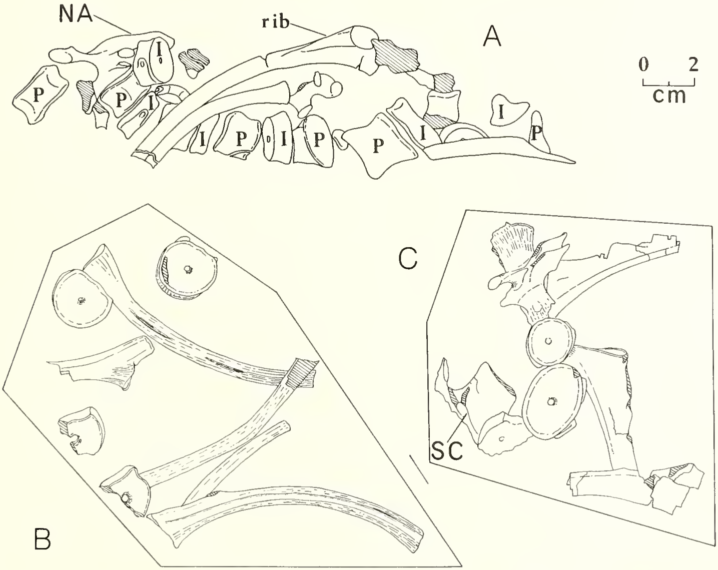
Specimen G15.73 (text-fig. 1A) consists of the complete articulated centra of seven successive dorsal vertebrae. This series commences anteriorly with the incompletely preserved pleurocentrum of the vertebra preceding the seven represented by both central elements. Dorsal and posterior to this pleurocentrum is a single, incomplete, neural arch, consisting of the neural spine, postzygapophyses, and right pedicel only. The articular heads, and most of the shafts, of two trunk ribs are also preserved, and lie on the morphologically left side of the vertebral series; that this is their true position is confirmed by the relationships between their tubercular and capitular heads. Almost all of the centra have undergone some degree of distortion due to compression during preservation; all except the two most anterior intercentra of the series therefore yield little useful information on the finer points of their structure.

Specimen G83.68 (text-fig. 1C) is a slab of shale bearing one pleurocentrum, one intercentrum, a third indeterminable central element, two incomplete neural arches, and the proximal parts of two trunk ribs. G83.68 was very briefly described by Atthey (1877, p. 374), who attributed it to *Pteroplax*.

Specimen G83.69 (text-fig. 1B) consists of a slab of shale on which are preserved two pleurocentra, two intercentra, and five incomplete ribs. Both intercentra and one pleurocentrum exhibit very large notochordal foramina; this, and other details of their structure, noted below, suggest that they are the centra of a juvenile individual.

Centrum. As is characteristic of the embolomerous condition in amphibian vertebrae, both pleurocentrum and intercentrum of *Pteroplax* form completely ossified discs of bone. Although the pleurocentra and intercentra of specimen G83.69 exhibit large notochordal foramina, these centra would appear from other features of their structure to be those of a juvenile individual, and it is probable that the dimensions of the foramina are related to this fact. In several of the articulated centra which compose specimen G15.73, the notochordal foramen would appear to have been occluded by growth of bone. Centra in which the foramen is so occluded have also been described in the eogyrinid embolomere *Eobaphetes kansensis* (Panchen 1977*a*), and large embolomerous centra with occluded notochordal foramina have been attributed to *Anthracosaurus russelli* (Huxley 1863; Panchen 1977*a*).

The pleurocentrum, which lies posterior to the intercentrum in the complete vertebra (text-fig. 3), is approximately circular in transverse section although somewhat flattened dorsally where it forms the floor of the neural canal. The pleurocentrum of *Pteroplax* has in all known specimens a much greater antero-posterior length than has the intercentrum, several of the pleurocentra of G15.73 being twice as thick as their respective intercentra. A similar disparity in thickness of pleurocentrum and intercentrum has been described in the vertebrae of the eogyrinid *Eogyrinus attheyi* (Panchen 1966), the Lower Permian archeriid *Archeria* (Case 1911), and the tiny *Calligenethlon watsoni* (Carroll 1967).



TEXT-FIG. 1. Presacral vertebrae and ribs of *Pteroplax cornutus* as preserved, × 0·5. A, diagrammatic representation of articulated vertebral series of specimen no. G15.73 in left lateral view; B, vertebrae and ribs of specimen no. G83.69; C, vertebrae and ribs of specimen no. G83.68. I, intercentrum; NA, neural arch; P, pleurocentrum; SC, supra-neural canal.

The pleurocentrum is deeply amphicoelous, both anterior and posterior articular faces being markedly concave. The anterior and posterior articular faces of the pleurocentrum have a surface of spongy bone, no covering of periosteal bone being present. The pleurocentrum shows no tendency to taper dorsally and has approximately the same antero-posterior length both dorsally and ventrally. Ventrally and laterally the circumference of the pleurocentrum has a coat of smooth periosteal bone which, in the case of the pleurocentra of specimen G83.69, is pierced by a number of nutrient or nerve foramina. The circumference of the pleurocentrum where it possesses a periosteal bone covering is strongly concave, with the result that the pleurocentrum is much constricted ventrally and laterally between its anterior and posterior faces. The median area of the dorsal surface of the pleurocentrum representing the floor of the neural canal lacks a surface of periosteal bone and is shallowly concave, forming a depression extending from the posterior to the anterior margin of the centrum.

In the anterior half of the dorsal surface of the pleurocentrum, and lying on either side of the depression marking the floor of the neural canal, there is a pair of facets for articulation with the pedicels of the neural arch. The articular faces of these facets are roughly elliptical in shape and are orientated in an antero-dorsal direction at an angle of approximately forty-five degrees. The two articular faces also have a very slight lateral inclination. The facets each project anteriorly a little way beyond the anterior rim of the pleurocentrum. Because of the antero-dorsal inclination of the articular faces of the two dorsal facets of the pleurocentrum, the posterior margin of each is considerably raised above the level of the floor of the neural canal and is supported on a stout buttress, the lateral surface of which has a covering of smooth periosteal bone. Details of the structure of the pleurocentrum will be apparent from text-fig. 2A-D.

The intercentrum (text-fig. 2E-H) is, like the pleurocentrum, a completely ossified disc of bone pierced longitudinally, at least in the case of juvenile individuals, by a notochordal foramen. It is, however, in all known cases considerably thinner than the pleurocentrum, having usually only about one-half of the antero-posterior length of the latter element. The intercentrum is, in an adult animal, almost circular in transverse section, although exhibiting dorsally a flattened antero-posterior strip of bone which represents the floor of the neural canal. The intercentrum of *Pteroplax* is less deeply amphicoelous than the pleurocentrum, the articular faces being markedly excavated only in the region immediately surrounding the notochordal foramen. The intercentrum would thus probably have had a 'ball and socket' type of articulation with the deeply amphicoelous pleurocentrum. Such an articulation between pleurocentrum and intercentrum has been noted in other embolomere genera by Panchen (1977*b*). The anterior and posterior articular faces of the intercentrum have a surface of spongy bone, as does the floor of the neural canal. The ventral and lateral portions of the circumference possess a covering layer of smooth periosteal bone which extends, in all the intercentra available for study, for approximately one-half of the height of the lateral surface of the centrum. It is probable, however, that this dorsal limit of the extent of the periosteal bone surface of the circumference of the intercentrum was not constant throughout the vertebral column. In *Eogyrinus* the height of the lateral periosteal bone of the intercentrum is known to decrease from front to back of the vertebral series, so far as the latter is known (Panchen 1966), and it is probable that this was also the case in *Pteroplax*.

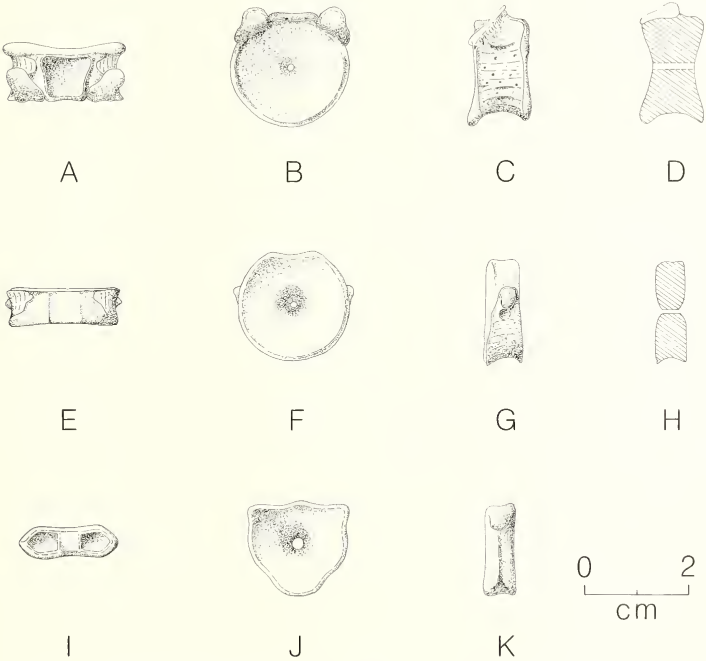
There is a shallow, roughly circular, concavity a little way ventral to the dorsal limit of the lateral periosteal bone of the intercentrum. A raised boss lies immediately dorsal and a little anterior to this depression. It is probable that one or both of these two structures was involved in the articulation of the capitular head of the rib. As no ribs are preserved in actual articulation with any known intercentrum of *Pteroplax*, it is not possible to be certain of the precise nature of this articulation. Panchen (1966) has noted that in the intercentrum of *Eogyrinus*, where a precisely similar arrangement of concavity and boss is present, the former appears to be situated too far ventrally to be the articular surface and that it may have served as the point of origin of a ligamentous structure holding the capitulum in articulation with, or behind, the boss.

The two intercentra present in specimen G83.69 (text-fig. 1B) are of especial interest because they appear to belong to a sub-adult individual of *Pteroplax*. This is strongly suggested by the relatively large size of the notochordal foramina of the centra, and by a number of other features of their structure. The circumference of each of the juvenile intercentra is flat or slightly convex, rather than concave, between the anterior and posterior articular faces of the element, and lacks any covering of smooth periosteal bone. In transverse section the intercentra do not approach the circular so closely as those characteristic of the adult animal, but terminate dorsally in an approximately horizontal surface which has a width very nearly as great as the diameter of the centrum itself. The over-all impression is that of a circle with a segment removed from its most dorsal part. A restoration of one of the juvenile intercentra of G83.69 is figured for comparison with the intercentrum of the adult animal (text-fig. 2I-K). The more fully preserved of the two juvenile intercentra bears, at the lateral extremity of the flattened dorsal surface, a massive laterally projecting boss. The capitular and tubercular heads of the ribs preserved in specimen G83.69 are well ossified and resemble those of the adult animal, and it would thus seem likely that the dorso-lateral boss of the intercentrum represents the site of articulation of the capitular head. If this is the case, as seems very probable, then this precocious development of the boss in the absence of a concavity ventral to it might be taken as indicating that the former structure formed the sole site of articulation of the capitulum of the rib in the adult intercentrum as well as in the juvenile.

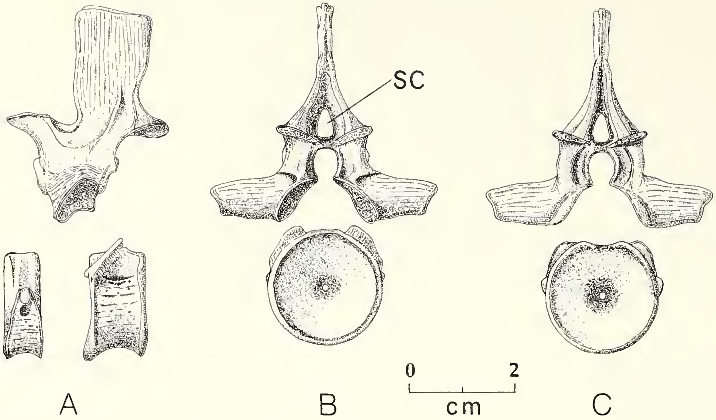
In all specimens available for study, the intercentra of *Pteroplax* show no tendency to taper dorsally (when seen in lateral view), but have approximately the same antero-posterior length dorsally as ventrally.

There is no evidence in any of the intercentra of *Pteroplax* available for study of the presence of any facets which may have served for an articulation of this element with the neural arch. As has been noted by Parrington (1967), to join the neural arch of an embolomerous vertebra securely to the intercentrum, as well as to the pleurocentrum, would be to reduce the flexibility of the vertebral column, thus abandoning the main advantage originally gained by diplospondyly.

Neural arch. Only fragmentary and relatively poorly preserved material representative of this structure is preserved in association with the vertebral centra attributed to *Pteroplax*. Three neural arches are thus preserved, one being associated with the most anterior pleurocentrum of the articulated length of vertebral column G15.73, and two further specimens being associated with the isolated centra of specimen G83.68. All



TEXT-FIG. 2. Presacral centra of *Pteroplax cornutus*, × 1. A–D, anterior trunk pleurocentrum in A, dorsal view; B, anterior view; C, left lateral view and D, longitudinal section; E–H, anterior trunk intercentrum in E, dorsal view; F, anterior view; G, left lateral view and H, longitudinal section; I–K, anterior trunk intercentrum of juvenile individual in I, dorsal; J, anterior and K, left lateral views.



TEXT-FIG. 3. Restoration of 'exploded' anterior trunk vertebra of *Pteroplax cornutus*, × 1. A, left lateral view; B, posterior view; C, anterior view. SC, supra-neural canal.

three neural arches have sustained some crushing during preservation and are somewhat distorted. No one of the three specimens is preserved in its entirety but, as the parts absent or unrecognizable in each neural arch are present in at least one of the other two specimens, and as all three appear to be those of presacral vertebrae, a composite reconstruction of the salient features of the neural arch of a trunk vertebra may be attempted with some confidence. Where details of structure are in doubt, as in the case of the form of the neural canal, these have been restored as in *Eogyrinus*. The morphology of the presacral neural arch of *Pteroplax* will be apparent from text-fig. 3.

The most interesting feature of the neural arch is the presence of a supra-neural canal in the ventral part of the neural spine. Owing to the absence of the dorsal part of the neural spine in the more completely preserved of the two neural arches of specimen G83.68, the supra-neural canal is open dorsally and forms a channel extending from between the prezygapophyses to the posterior part of the neural spine between the postzygapophyses. In the second of the two neural arch specimens of G83.68, which consists of the neural spine and right prezygapophysis only, the former has been split vertically and the right lateral wall of the supra-neural canal is exposed to view (text-fig. 1C). It is clear from this specimen that the walls of the supra-neural canal have a lining of smooth periosteal bone.

The structure of the neural arch of a presacral vertebra of *Pteroplax*, as revealed by the available material, is, except for the presence of the supra-neural canal, very similar to that of *Eogyrinus* as described by Panchen (1966). The neural arch of *Pteroplax* is, as might be expected from the dimensions of the centra, considerably smaller than that of *Eogyrinus*, being approximately one-half the size of those of the latter genus. It would appear that the neural arch of *Pteroplax* is also a rather more gracile structure than that of *Eogyrinus*.

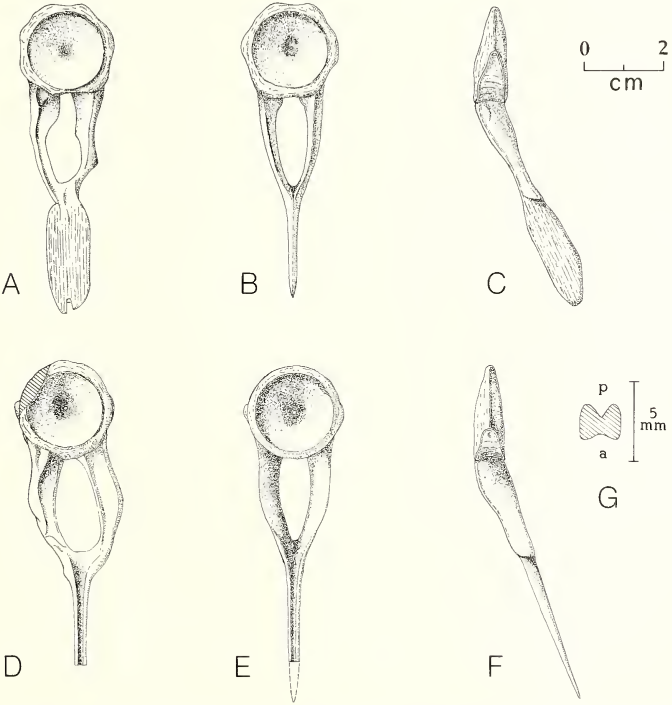
The mode of articulation of the intercentrum, pleurocentrum, and neural arch will be evident from the restoration of these three elements in text-fig. 3.

Regional variation. The paucity and the poor state of preservation of the known vertebral material of *Pteroplax* are such that the identification of regional variation within the dorsal vertebral column is not possible with any degree of certainty. The only articulated series of vertebrae available for study, specimen G15.73, consists of the complete centra of only seven successive dorsal vertebrae and it is not likely that any regional variation originally present within the vertebral column of *Pteroplax* will be readily apparent in so short a series. Panchen (1966) has described a number of trends present in the vertebral column of *Eogyrinus* and it seems probable that similar regional variations in form of the vertebrae were present also in *Pteroplax*.

CAUDAL VERTEBRAE

Two isolated caudal intercentra, from the Low Main Seam at Newsham, are attributed, on grounds of size, to *Pteroplax* and yield useful information as to the structure of the tail in this form.

Specimen G4.83 (text-fig. 4A–C) consists of the intercentrum of a proximal caudal vertebra, with a fused haemal arch bearing a short, blade-like haemal spine. It is preserved in posterior view, the anterior face of the intercentrum lying within the matrix which surrounds the specimen. The intercentrum and haemal arch have suffered some post-mortem compression and the arch has been twisted in such a way that the left lateral face of the haemal spine now faces posteriorly. The specimen bears a remarkable resemblance in both structure and mode of preservation to a much larger, isolated caudal intercentrum and haemal arch of *E. attheyi* described and figured by Watson (1926, fig. 23).



TEXT-FIG. 4. Caudal intercentra of *Pteroplax cornutus*. A–C, proximal caudal intercentrum of specimen no. G4.83 in A, posterior view as preserved; B, posterior view, restored and C, left lateral view, restored; D–F, distal caudal intercentrum of specimen no. G86.61 in D, posterior view as preserved; E, posterior view, restored and F, left lateral view, restored; G, transverse section of haemal spine of specimen no. G86.61. A–F, × 0·6; G, × 3. a, anterior; p, posterior.

The intercentrum possesses a posterior articular face which, like those of the trunk intercentra, is markedly concave only in the immediate vicinity of the small notochordal foramen. The centrum appears to become thinner dorsally, tapering when seen in lateral view. A covering of smooth periosteal bone would appear to have extended approximately half-way up the lateral surface of the intercentrum. This finished area is strongly concave and appears, like the centrum itself, to taper dorsally. It is uncertain whether or not a facet for the capitular articulation of a caudal rib is present in specimen G4.83.

Ventrally, the intercentrum bears a large haemal arch, the pedicels of which enclose a spacious haemal canal which has, in cross-section, the form of a vertically elongated oval. The haemal spine itself is a broad blade-like structure, compressed laterally and bearing a number of fine vertical striations.

In *E. attheyi* the haemal arches and spines of the proximal caudal vertebrae are directed posteriorly as well as ventrally (Panchen 1966) and a similar orientation of these structures has been restored in the reconstructions of the caudal intercentra of *Pteroplax* (text-fig. 4B–C, E–F).

Specimen G86.61 (text-fig. 4D–G) consists of the intercentrum and fused haemal arch of a caudal vertebra more distal than that of specimen G4.83. The intercentrum has a diameter of approximately 24·0 mm. The relatively large size of the intercentrum, despite its presumed distal position in the tail, makes attribution to *Pteroplax* uncertain. It is possible that the specimen in fact belongs to the larger *Eogyrinus*, its small diameter when compared with typical trunk centra of this form being due to its original situation in the distal part of the caudal vertebral series. It is, however, equally possible that it pertains to a large specimen of *Pteroplax* and it will be here described as belonging to this genus.

As is the case in specimen G4.83, the intercentrum appears to taper dorsally when seen in lateral view. The vertical extent of the lateral covering of smooth periosteal bone is uncertain, and this has been restored as extending only a very short distance above the base of the haemal arch pedicel. In specimen G86.61 the haemal spine is not laterally compressed but forms a truly spine-like structure, roughly quadrangular in transverse section. The haemal spine bears a distinct longitudinal groove on both anterior and posterior faces, the posterior groove being apparently the deeper and better defined of the two (text-fig. 4G). The haemal spine of G86.61 is unfortunately broken off short approximately 30·0 mm from its origin at the point of fusion of the arch pedicels, and it is thus not possible to estimate with certainty its original length.

Case (1911, fig. 51G) figured (as '*Cricotus*') a series of articulated distal caudal vertebrae of *Archeria*. The intercentra of the vertebrae appear to bear postero-ventrally directed elongate and tapering haemal spines below the haemal arches present. These structures, although all broken and lacking their distal parts, appear to closely resemble that present in intercentrum G86.61 of *Pteroplax*. It is, however, not possible to ascertain from Case's figure whether the haemal spines of *Archeria* are also quadrangular in section.

The haemal arches and spines of the proximal caudal vertebrae of *Pteroplax*, such as are shown by specimen G4.83, presumably served for the support of the ventral part of a laterally compressed tail. Haemal arches of this type have been described in *Eogyrinus* (Watson 1926; Panchen 1966), where they are matched dorsally by neural arches bearing neural spines of normal laterally compressed type. The elongate haemal spines of the distal caudal vertebrae of *Archeria* and *Pteroplax* may have served to support the distal part of a laterally compressed tail and the ventral part of a distinct caudal fin. The neural arches of the caudal vertebrae of *Archeria* figured by Case (1911) bear posteriorly inclined elongate neural spines and Romer (1956) has described the presence in this form of a dorsal caudal fin supported by either the neural spines of the distal caudal vertebrae or by supra-neural spines articulating with them. A caudal fin, both epaxial and hypaxial in extent, has been restored in *Eogyrinus* by Panchen (1972) and it seems highly probable that a similar fin was present in at least the distal region of the tail in *Pteroplax*.

RIBS

In the collections of the Hancock Museum are a large number of isolated ribs belonging to 'labyrinthodont' amphibians, from the Low Main Seam at Newsham. The majority of these ribs may be placed in one or other of two distinct size ranges. Panchen (1966), noting this fact, has suggested that those ribs in the larger category most probably belong to *Eogyrinus* and the contemporary loxommatid *M. pachycephalus* (Barkas), and those in the smaller size range to *Pteroplax*. On the basis of this hypothesis, a series of large trunk and caudal ribs, many of which were also definitely associated with *Eogyrinus* specimens, were described (Panchen 1966) as belonging to that genus.

It would seem more likely, however, considering the relatively small size of the skull of *M. pachycephalus* (Beaumont 1977), for which unfortunately no certainly attributable postcranial remains are known, that if any ribs of this species are represented amongst the Hancock Museum collections from Newsham, these would fall into the smaller size range, with those of *Pteroplax*. There can be little doubt that the ribs of *Pteroplax* are of the smaller type. Two ribs of this size are preserved with the lectotype skull table of *Pteroplax*, and a number of rib specimens are associated with various of the vertebrae attributed to this form, including the articulated length of vertebral column G15.73.

In the absence of any description of the morphology of the ribs of *Megalocephalus*, it is not possible to determine with certainty which, if any, of the smaller isolated ribs from Newsham belong to this genus rather than to *Pteroplax*. Although the trunk ribs of some Permian temnospondyls such as *Eryops* bear well-developed uncinate processes, there is no real reason to suppose that the ribs of *Megalocephalus*, which was probably largely aquatic in habit, might be expected to exhibit these structures and thus be distinguishable from those of anthracosaurs such as *Pteroplax*. Neither may the apparent absence of any *Megalocephalus* vertebrae from the Hancock Museum's Newsham collections be cited as reason to suppose that the ribs of this form might also be rarely, if at all, represented. If, as has been postulated by Romer (1947) and at least partly vindicated by Baird (1957), the loxommatids possessed vertebrae of rhachitomous type, the rarity of *Megalocephalus* vertebrae from Newsham might be explained as due to the dissociation of the relatively small, and easily overlooked, central elements subsequent to the death of the animal.

Because it would thus appear impossible to distinguish between isolated ribs of *Pteroplax* and *Megalocephalus*, the ribs described below as belonging to the former genus have, whenever possible, been selected from those associated with the embolomerous vertebrae attributed to this form. Several of the isolated ribs described as those of *Pteroplax* do, however, closely resemble those described for *Eogyrinus* by Panchen (1966).

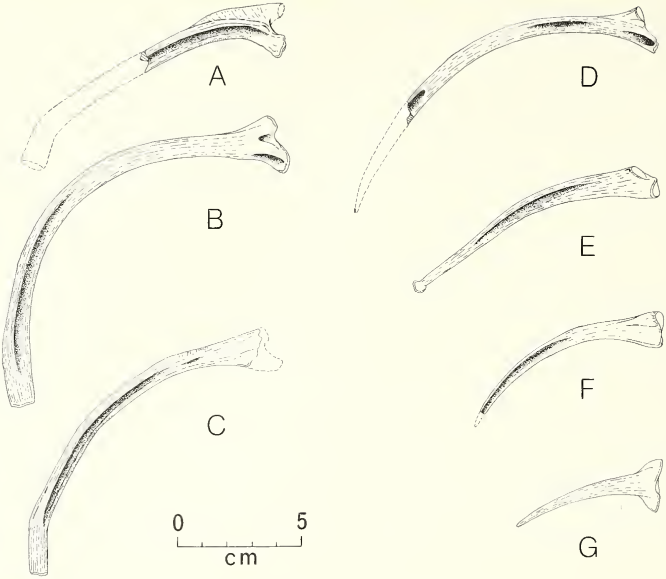
The ribs of *Pteroplax* are dichocephalous in typical early tetrapod manner, exhibiting in the articular head a tubercular facet, usually slightly concave, for the reception of the diapophysis of the neural arch and, ventral and usually slightly anterior to this, a capitulum continuing the curvature of the rib shaft and articulating with the intercentrum of the vertebra. In the more anterior members of the presacral series of ribs the capitulum is situated mesial to the tuberculum of the rib head but, correlated with the presumed posterior decrease in the transverse span of the diapophyses of the vertebrae, the two articulations of the rib approach closer to the same vertical plane in the more posterior members of the series. The radius of curvature of the rib shaft varies according to the position occupied by the rib in the presacral vertebral column. In specimen G15.76 (text-fig. 5B), a rib from the anterior trunk or 'thoracic' region of the body, the shaft clearly extends as far as the lateral margins of the ventral body surface. It is likely that, as in many modern Crocodilia and the more unspecialized members of the Lepidosauria, the more anterior trunk ribs continued distal to their ossified extremities in cartilage and articulated ultimately with a cartilaginous sternum extending posteriorly from the interclavicle.

The shaft of an anterior trunk rib is expanded in the region of the articular head, a dorsal extension of the shaft extending posteriorly and dorsally, and linking the shaft proper and the tuberculum of the rib. The structure of this region is clearly evident from the more anterior of the two ribs preserved in association with specimen G15.73 (text-fig. 1A). As in *Eogyrinus* (Panchen 1966), the postero-dorsal surface of the rib in this region is deeply concave, the concavity extending for a distance of several centimetres lateral and ventral to the tubercular facet. In the majority of the anterior trunk ribs available for study, the postero-dorsal concavity of the articular head region is continued as a shallow longitudinal groove extending for the greater part of the length of the shaft. The shaft in all specimens lacks any evidence of the presence of an ossified uncinate process, and in this respect corresponds to the pattern apparently common to all Batrachosauria.

Seven of the isolated ribs from Newsham attributed to *Pteroplax* are figured (text-fig. 5A–G) in an attempt at restoration of a series of presacral ribs, showing the modifications in structure characteristic of different regions of the trunk. The resemblance of certain of the ribs in this series, and in particular of the more posterior members, to the much larger rib specimens figured by Panchen (1966) for *Eogyrinus* is noteworthy and might be taken as some confirmation of the correctness of the attribution of these ribs to *Pteroplax*.

The first and most anterior rib of the figured series (text-fig. 5A), specimen G83.73, is placed in this position, with some reserve, largely because of its apparent resemblance to a rib specimen of *E. attheyi* figured by Panchen (1966) as possibly representing an anterior member of the rib series underlying the pectoral girdle in that species. Like the latter specimen, the rib attributed to *Pteroplax* is characterized by the presence of a blade-like postero-dorsal extension of the proximal shaft, which may have served to support part of the endochondral shoulder girdle.

The apparently widely separated tubercular and capitular facets of G83.73 would appear to debar this specimen from representing a posterior trunk rib, but it is interesting to note that in the seymouriamorph *Kotlassia* the proximal caudal ribs exhibit similarly widely separated articular facets (Bystrow 1944), as, indeed, do those of *Eogyrinus* (Panchen 1966). It is possible, therefore, that G83.73 actually represents an incompletely preserved caudal rib.



TEXT-FIG. 5. Series of trunk ribs of *Pteroplax cornutus* in reconstructed anterior-posterior sequence, ×0·5. A–C in anterior view, D–F in posterior view. A, pectoral rib specimen no. G83.73; B, 'thoracic' rib specimen no. G15.76; C, 'thoracic' rib specimen no. G15.78; D, 'thoracic' rib specimen no. G15.80; E, 'lumbar' rib specimen no. G83.72; F, 'lumbar' rib specimen no. G83.74; G, immediately presacral rib specimen no. G15.77.

DISCUSSION

In most respects the vertebrae of *Pteroplax* conform to the pattern described by Panchen (1966) in *Eogyrinus*. In two points of structure, however, the vertebrae of *Pteroplax* differ from those of the latter genus.

In at least the trunk region, the intercentra of *Pteroplax* are as thick in their dorsal part as ventrally. In this feature the intercentra resemble those of *Archeria*, which, as indicated by the figures of Case (1911, fig. 51), also retain the same thickness throughout their height. The condition of the intercentrum in *Pteroplax* and *Archeria* is, however, in contrast to that present in *E. attheyi*. In this last species the intercentrum is usually wedge-shaped in lateral view, the anterior and posterior faces meeting dorsally (Panchen 1966). Whether the apparent similarities in the intercentra of *Pteroplax* and *Archeria* are of any phylogenetic significance is uncertain. The less completely ossified nature of the intercentra of *Eogyrinus* may be related merely to the much larger size of this form, the centra of which typically have a diameter approximately twice that of those of *Pteroplax*. It is, however, of interest to note at this point that the intercentra of the vertebrae of the North American Pennsylvanian embolomere *Cricotus* (Cope 1875), which are of approximately the same diameter as those of *Archeria* and *Pteroplax*, differ from those of the last two genera in being, as noted by Romer (1947), 'pinched dorsally', presumably in a manner similar to the intercentra of *Eogyrinus*.

It is, however, also possible that the degree of ossification of the intercentra may be related to their position within the vertebral column or to the age of the individual animal, and it would thus be unwise to attempt to draw any definite conclusions from the apparent resemblance of the intercentra of *Pteroplax* to those of *Archeria* and the differences between these genera and *Eogyrinus* and *Cricotus*. It may nevertheless be noted that the presumed juvenile intercentra of *Pteroplax*, described above, show no tendency to taper dorsally.

Aside from the differences in absolute size and proportion, the only apparent point of significance in which the dorsal neural arch of *Pteroplax* differs from that of *Eogyrinus* lies in the presence in the former genus of a longitudinal supraneural canal piercing the neural spine of the arch dorsal to the neural canal proper. The supraneural canal is separated from the neural canal by a thin floor of bone.

Case (1915) figured (as '*Cricotus*') a neural arch of the Lower Permian embolomere *Archeria* in which, although the dorsal part of the neural spine is absent, a supraneural canal similar to that present in the vertebrae of *Pteroplax* is clearly present (Case 1915, pl. 22, fig. 1). Case noted the presence of such a supraneural canal in several further *Archeria* dorsal vertebrae, noting also that the canal appeared to have a greater cross-sectional area in those vertebrae possessing wide diapophyses than in those in which the diapophyses were relatively short. In *Eogyrinus* the anterior trunk vertebrae are characterized by the possession of diapophyses of greater lateral extent than those present in the more posterior trunk region (Panchen 1966) and it seems probable that a similar condition existed in *Archeria*. This being the case, it would appear from the information given by Case (1915) that the supraneural canal in *Archeria* is developed to a much greater degree in the anterior trunk vertebrae than in the posterior members of the vertebral series. Case also noted that the supraneural canal is not present as such in the case of a number of the more posterior trunk vertebrae of *Archeria* available to him, being represented only by a deep pitting of the anterior and posterior surfaces of the neural spine, and that this is also the case in the sacral vertebra.

In *E. attheyi* the neural spine is excavated anteriorly and posteriorly by a dorsally tapering groove, corresponding in position to the supraneural canal of *Pteroplax*, but the two depressions, anterior and posterior, are not known to join to form a continuous canal in the vertebrae of this species.

The function of the supraneural canal of *Pteroplax* and *Archeria* is not certainly known. Embryologically, the neural arches of vertebrates typically arise as paired structures which grow upward and mesially to fuse above the spinal cord, and it is thus possible that the supraneural canal in the vertebrae of the two above genera represents the partial retention of an ontogenetic stage prior to complete fusion of the two neural arch elements. However, it does not appear likely that the presence of this canal in *Pteroplax* and *Archeria* may be explained as due to the vertebrae which exhibit it being those of juvenile individuals. The dorsal vertebra of *Archeria* figured by Case (1915) as exhibiting a supraneural canal has the neural arch firmly attached to the pleurocentrum, and this, and the small size of the notochordal foramen of the centrum, do not suggest that the vertebra is that of a juvenile animal. The centra associated with the known neural arches of *Pteroplax* also possess small, or possibly occluded, notochordal foramina and would therefore appear to be those of well-grown individuals. Furthermore, the surface of periosteal bone which is present on the walls of the supraneural canal in *Pteroplax* suggests that this space does not simply represent an unossified area of the neural spine, occupied in life by cartilage, but that it served some more definite function.

Case (1915) suggested that the supraneural canal of *Archeria* was occupied in life by a longitudinal ligament or ligaments, extending as a continuous structure through the neural arches of the majority of the series of presacral vertebrae. In the case of the (usually posterior) vertebrae in which the canal was represented only by deep anterior and posterior pitting of the neural spine, the course of the ligament was assumed to be interrupted, extending only between successive vertebrae. This interpretation of the function of the supraneural canal of *Archeria* appears to be the most likely. *Archeria* is known to possess an elongated presacral vertebral column of approximately forty vertebrae (Romer 1947) and the presence of the continuous longitudinal ligament postulated by Case may be correlated with this fact, the ligament serving to compensate for the weaknesses inherent in such a long vertebral series, even in an aquatic animal like *Archeria*. If this is indeed the case, then the presence of a supraneural canal in *Pteroplax* is a feature of some interest.

As noted above, no supraneural canal has been described in the vertebrae of *E. attheyi*. This species has been restored by Panchen (1966, 1972) as possessing a presacral vertebral column of approximately forty vertebrae and, if the supraneural canal of *Archeria* and *Pteroplax* does indeed serve for the passage of a longitudinal ligament acting as a tension member to strengthen an elongate presacral vertebral series, the absence of this structure in *Eogyrinus* is somewhat surprising. It is, however, interesting to note that the presacral vertebral column of *Eogyrinus* is known from no specimen comprising more than twenty-four individual vertebrae (Panchen 1966).

Neither a supraneural canal in the dorsal vertebrae, nor a degree of elongation of the presacral column even approaching that of *Archeria* (which has forty vertebrae) has been described in any member of the larger of the two embolomere lineages postulated by Romer (1963). It is tempting to speculate, in the absence of any positive evidence to the contrary, that these specializations may have been restricted to the smaller of Romer's suggested lineages. The number of presacral vertebrae present in *Pteroplax* is, however, unknown and, although the presence of a supraneural canal in this form suggests, if the interpretation of its function which is suggested above is correct, some elongation of the dorsal vertebral column, this may not have been so great as in the Lower Permian *Archeria*, the length of whose dorsal region may perhaps represent the culmination of trends originating in the Carboniferous forms ancestral to it. Certainly it is difficult to conceive of the earliest embolomeres exhibiting a 'jump' from the approximately twenty-four presacral vertebrae apparently primitive for 'labyrinthodont' amphibians (Romer 1947) to the forty known to be present in *Archeria* without any intermediate stages. It is unfortunate that the nature of the known specimens of Carboniferous embolomeres so far described makes it impossible to be certain of the degree, if any, of elongation of the dorsal vertebral column present in these forms.

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A NEW PTERASPIDID OSTRACODERM FROM THE DEVONIAN SENNI BEDS FORMATION OF SOUTH WALES AND ITS STRATIGRAPHIC SIGNIFICANCE

by E. J. LOEFFLER *and* R. G. THOMAS

ABSTRACT. A pteraspidid ostracoderm, *Althaspis senniensis* sp. nov., is described from the Senni Beds Formation of central south Wales. An associated assemblage of dispersed miospores indicates a mid Middle to lower Upper Siegenian age for this fossil. A typical Breconian macroflora is also present. The Dittonian aspect of the ostracoderm supports the suggestion that there is overlap between the Dittonian and Breconian Stages of the Lower Old Red Sandstone.

THE pteraspidid ostracoderm described herein was found by Dr. D. Goujet (Paris), in a fallen block of blue-grey mudstone on the floor of the disused Heol Senni Quarry, Powys, south Wales. This quarry was visited during the course of one of the post-symposium field excursions (Excursion B2) which formed part of the programme of the Palaeontological Association's Devonian Symposium (PADS), held in Bristol in September 1978. The quarry, which is situated on the north-eastern face of Fan Bwlch Chwyth (SN 9145 2210), 7 km south of Sennybridge, exposes a near flat-lying, sandstone-dominated sequence within the upper Middle part of the Senni Beds Formation; the succession is described by Edwards *et al.* (1978) in the field guide to the excursion.

The block containing the pteraspidid is of unlaminated, blue-grey mudstone and was found amongst other fallen debris at the base of the main quarry face; its original position in the sequence is uncertain. The pteraspidid plates, including a ventral disc, rostral plate, branchial plate, and some scales, were disarticulated but found in close proximity to one another on the same surface, within an area of 400 cm^2. Careful splitting of the block yielded a single, unidentifiable plant fragment, but no additional fish material.

Palaeontology of Heol Senni Quarry

Flora. Plant fragments are common within the Senni Beds Formation at Heol Senni Quarry. Vegetative vascular macroplant axes several centimetres long are preserved as carbonaceous compressions in some blue-grey to grey-green coloured, very fine grained siltstone units. Examples of cf. *Psilophyton princeps* (Croft and Lang 1942) and *Hostinella* have been found in loose blocks of blue-grey, fine-grained sandstone and siltstone on the quarry floor. Additional fertile material collected during the PADS excursion has been identified by D. Edwards (pers. comm. 1979) as *Gosslingia breconensis* Heard and *Zosterophyllum* sp. She drew attention to the similarity between the Heol Senni flora and that of the Brecon Beacons Quarry, where all of these taxa are found, and of Llanover, where *Gosslingia* and cf. *P. princeps* occur.

In comparing the Cosheston Group of south-west Dyfed with the Senni Beds, Thomas (1978*a*) recognized over fifty taxa of dispersed miospores from Heol Senni. Important constituents of his assemblage include: *Calamospora atava* (Naum.) McGregor, 1964; *C. pannucea* Richardson, 1965; *Leiotriletes pagius* Allen, 1965; *Retusotriletes frivolus* Chibrickova, 1959; *R.* cf. *R. pychovii* Naumova, 1953; *R. triangulatus* (Streel) Streel, 1967; *Apiculatasporites* cf. *A. perpusillus* (Naum.) McGregor, 1973; *A. arenorugosa* McGregor, 1973; *A.* cf. *A. brandtii* Streel, 1964; *A.* cf. *A. plicata* (Allen) Streel, 1967; *A.* spp. nov.; *Dibolisporites* cf. *D. eifeliensis* (Lanninger) McGregor, 1973;

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D. sp. nov.; *Emphanisporites* cf. *E. micrornatus* Richardson and Lister, 1969; *E. ?neglectus* (Vigran) *sensu* McGregor, 1973; *E. obscurus* McGregor, 1961; *E. rotatus* (McGregor) McGregor, 1973; *Aneurospora minuta* McGregor, 1973; *Aneurospora* comb. nov. et vars. nov.; *Camptozonotriletes* cf. *C. caperatus* McGregor, 1973; *Clivosispora torquata* McGregor, 1973 var. nov.; *?Lycospora* sp. nov.; and *Archaeozonotriletes chulus* vars. *chulus* and *nanus*. Other genera represented within these assemblages include: *Punctatisporites*; *Acanthotriletes*; *Anapiculatisporites*; *Apiculatisporis*; *Verrucosisporites*; *Convolutispora*; *Dictyotriletes*; *?Iberoespora*; *Stenozonotriletes*; and *Ambitisporites*. Several Heol Senni miospore samples contain derived Tremadocian and Wenlockian acritarchs.

On the basis of palynology and lithofacies, Thomas (1978*a*) considered the Senni Beds Formation to be the facies equivalent of the lower and middle portions of his Mill Bay Formation of the Cosheston Group, and its age to be mid Middle to lower Upper Siegenian.

Fauna. The ostracoderm fish which is described here is the best preserved and most complete yet recovered from the Senni Beds, and the first to have been found at Heol Senni Quarry. Vertebrates are extremely rare in the Senni Beds, having been recorded from only two other sites. The enigmatic *Pteraspis dixoni* White, considered by White (1938, 1950) to be a very primitive pteraspidid, occurs together with *Cephalaspis* sp. indet, low down in the Senni Beds near Ferryside in Carmarthenshire; *Rhinopteraspis cornubica* (McCoy) has been found high in the Senni Beds of Primrose Hill Quarry, near Crickhowell, Powys (White 1938).

SYSTEMATIC PALAEONTOLOGY

Family PTERASPIDIDAE White, 1935
Subfamily PTERASPIDINAE Denison, 1970
Genus ALTHASPIS Zych, 1931

Diagnosis. See Dineley and Loeffler (1976, p. 129).

Type species. *Pteraspis elongata* Zych (non Alth) = *Althaspis samsonowiczi* Tarlo.

Other species. *A. anatirostra* Blieck, *A. kujdanowiensis* (Stensiö), *A. leachi* (White), *A. longirostra* (Zych), *A. spathulirostris* (Stensiö), *A. vimiensis* White.

Althaspis senniensis sp. nov.

Plates 35 and 36

Derivation of name. From Heol Senni.

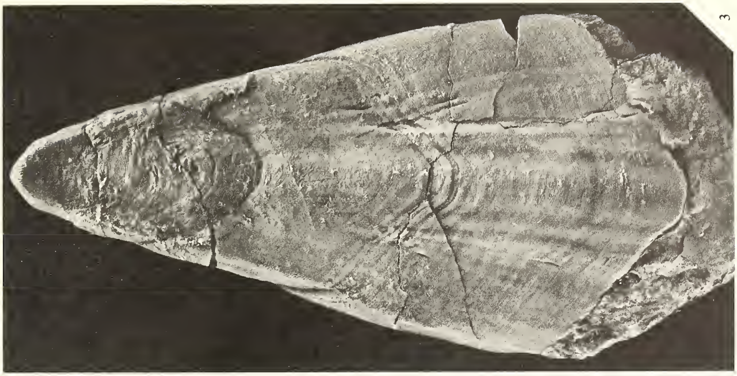
Diagnosis. Rostrum long and tapered (median length of rostral plate = 56 mm), with antero-lateral margins converging at approx. 35°. Subrostral surface covered in dentine ridges which are largely, but variably, deflected forward in the longitudinal mid-line.

Holotype. A rostral plate, BMNH P.59744a, plate 35, figs. 2 and 3.

Other material. A ventral disc, BMNH P.59744b, pl. II, fig. 5. An incomplete branchial plate, BMNH P.59744c, pl. 35, fig. 1. Nine disarticulated scales, BMNH P.59744d–l, pl. 36, figs. 1–4.

EXPLANATION OF PLATE 35

Figs. 1–3. *Althaspis senniensis* sp. nov. 1, Incomplete branchial plate (BMNH P.59744c), ×2·5 approx. 2, Rostral plate in ventral view, showing subrostral surface (BMNH P.59744a, holotype), ×2·3 approx. 3, Rostral plate in dorsal view (BMNH P.59744a, holotype), ×2·3 approx.



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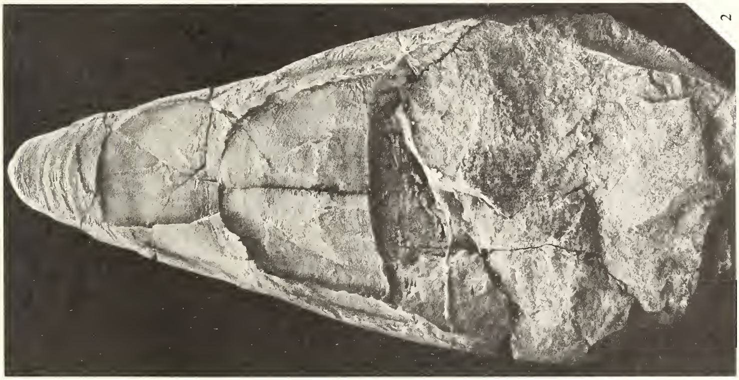

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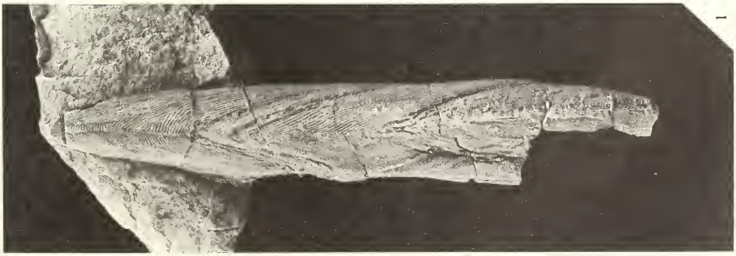


1

LOEFFLER and THOMAS, Pteraspidid ostracoderm

Description

Rostral plate (Pl. 35, figs. 2, 3). The rostral plate has a median length of 56 mm and a maximum width of 28 mm. The free, antero-lateral margins converge at an angle of approximately 35°; the postero-lateral margins, which would presumably have been in contact with the orbital and pineal plates, converge at an angle of about 105°. On the dorsal surface of the rostrum, the dentine ridges have a density of approximately 7·5 mm; the surface of the plate is subdivided into three distinct areas by two deep grooves, which are interpreted as growth lines. Within the more posterior of these three divisions, ridges are concave forward (i.e. deflected backwards in the longitudinal mid-line), arranged parallel to the postero-lateral margins. Within the central division, the backward deflection of the ridges is increased, but reduced again at the rear of the anterior division. The curvature of the ridges increases toward the extremity of the rostrum, to become almost concentric around the tip.

On the underside of the rostrum the ventral preoral surface extends back some 30 mm (over half the total length of the rostral plate). This surface is covered with dentine ridges which are continuous with the dorsal ornament. The growth lines can also be traced ventrally, producing three slightly less distinct subdivisions. Posteriorly, the ridges are transverse to weakly convex forwards (i.e. deflected forwards medially), becoming more strongly convex in the central area. Anteriorly, the ridges change from being convex, to become transverse or slightly concave right at the tip of the rostrum.

There is no indication of an ascending lamella but, as the posterior margin of the preoral surface is discordant to the ridge pattern, it is possible that this is a broken edge. This is difficult to confirm, as the bone is crushed. The whole preoral part of the rostrum is rather thin, suggesting that the cancellous layer has been completely crushed.

Branchial plate (Pl. 35, fig. 1). The anterior 46 mm of the branchial plate is preserved; its maximum width is 7·5 mm. Dentine ridges, with a density of 6–8 mm converge on the longitudinal mid-line, toward the anterior end of the plate.

Ventral disc (Pl. 36, fig. 5). The ventral disc is approximately 87 mm long, with a maximum width of 50 mm being achieved about 25 mm behind the anterior margin, and a minimum width of 38 mm about 18 mm in front of the posterior margin. The plate is vaulted both longitudinally and transversely, most strongly at its narrowest part. The anterior margin is broadly rounded, the posterior margin is incomplete. Ornamentation is of rather flat-topped dentine ridges with weakly developed lateral crenulations; ridge density varies from 4·5 to 7·5 per mm, coarsest ornament being developed anteriorly and medially. The pores of the lateral line system are barely visible, but several growth lines are distinguishable.

Scales. Three distinct types of scale are recognized:

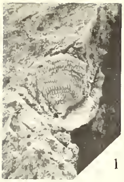
1. Lateral scales (Pl. 36, figs. 1, 2). Represented by seven specimens, these are flat, rhomb-shaped scales which are in the order of 4–5 mm long and 4–5 mm wide, and which have a narrow overlap brim anteriorly.
2. Fulcral scales (Pl. 36, fig. 3). Represented by a single specimen which is long (12 mm) and narrow (3 mm) and strongly arched about the mid-line.
3. Ridge scales (Pl. 36, fig. 4). Again strongly arched about the mid-line, this unique scale is of similar length to the fulcral scale, but almost twice as wide.

Discussion. The mode of preservation of this material suggests that all of the plates and scales belonged to a single individual, which had not been transported a great distance after death. The fact that the rostral plate is disarticulated suggests that it was weakly, or incompletely attached to the rest of the dorsal shield; these could be the remains of an immature, or recently mature individual.

Pteraspidid classification relies heavily on the morphology of the subrostral surface (Tarlo 1961; Denison 1970; but see Novitskaya 1975, for an alternative view). The presence of an extensive subrostral surface covered in dentine ridges which are continuous with those of the dorsal surface is the basis for referring the Heol Senni specimen to the genus *Althaspis*.

EXPLANATION OF PLATE 36

Figs. 1–5. *Althaspis senniensis* sp. nov. 1, Lateral scale (BMNH P.59744d), ×3 approx. 2, Lateral scale (BMNH P.59744e), ×3 approx. 3, Fulcral scale (BMNH P.59744k), ×2·7 approx. 4. Ridge scale (BMNH P.597441), ×2·7 approx. 5, Ventral disc (BMNH P.59744b), ×2 approx.



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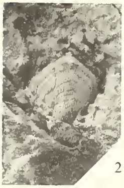

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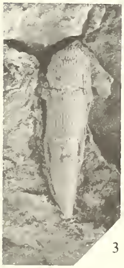

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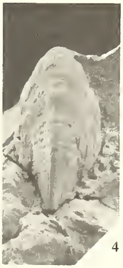

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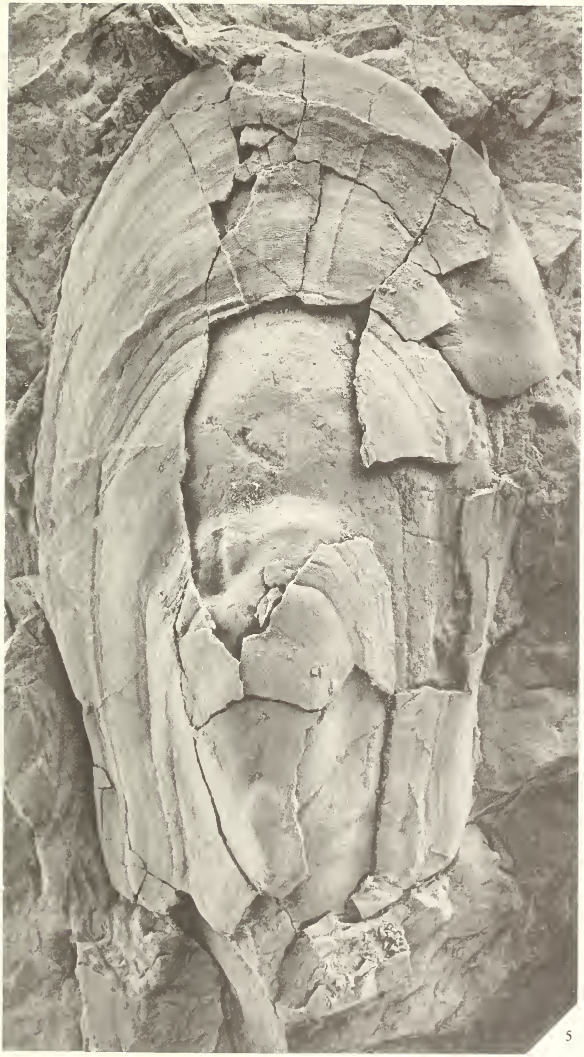

5

LOEFFLER and THOMAS, Pteraspidid ostracoderm

Only one species of *Althaspis* has previously been recorded from Britain, and that is the late Dittonian zonal form, *A. leachi* (White), now known from south-west Dyfed (White 1938), the Clee Hills (Ball and Dineley 1952), and the Forest of Dean (Allen *et al.* 1968). Rice (1967), describing them as *Rhinopteraspis cornubica*, recognized two forms of rostral plate amongst the specimens from Mitcheldean in the Forest of Dean: a long, narrow form and a squat form, in which the breadth to length ratios are 0·29–0·34 and 0·38–0·40 respectively (calculated from Rice's published data). Referring to additional material, but without publishing detailed palaeontological descriptions, Allen *et al.* (1968) re-identified the Mitcheldean pteraspidid as *A. leachi*; they agreed that two types of rostrum were present, figuring BMNH P.49119 (p. 146, fig. 2*d*) as an example of the squat form. Although it is approximately 1·3 times longer, this particular specimen is close in shape to the rostral plate from Heol Senni. Examination of material in the collections of the British Museum (Natural History), however, revealed the specimen to be somewhat atypical of the squat rostra from Mitcheldean; typical examples (e.g. P.49183, P.49186) are about 100 mm long and 40 mm wide (width ratio 0·40), while the specimen figured by Allen *et al.* (1968, fig. 2*d*) is about 75 mm long and 35 mm wide (width ratio 0·46). Ventral discs of *A. leachi* show little variation in shape and proportion (Rice 1967). At 136 mm, the median length of the ventral disc figured by Rice (1967, fig. 11) is approx. 1·6 times greater than that of the ventral disc from Heol Senni; the width ratios of the Mitcheldean and Heol Senni ventral discs are also quite different, being 0·42 and 0·57 respectively.

Other species of *Althaspis* are known from Belgium, Spitsbergen, and Podolia (Ukraine). On the basis of rostral shape alone, the Heol Senni material is readily distinguishable from *A. anatirostra* (Blieck 1975) and *A. spathulirostra* (Stensio 1964). The remaining species, all of which have rather long, tapered rostra, are more difficult to separate, largely because the Podolian species have not been adequately defined or described. In size, the rostrum from Heol Senni resembles a small, possibly juvenile, rostrum which White (1960) referred to *A. vimiensis*; in that species, however, the rostrum is more robust and has a more bluntly rounded tip.

A striking feature of the Heol Senni rostrum, and one in which it apparently differs from all of the other species except *A. leachi*, is the irregularity and curvature of the subrostral ridges; in other species, the ridges seem to be regular and more transverse.

As the pteraspidid from Heol Senni cannot readily be accommodated elsewhere, a new species, *A. senniensis*, has been established to receive it.

DEPOSITIONAL ENVIRONMENT OF THE SENNI BEDS FORMATION

The Senni Beds Formation crops out from the head of Carmarthen Bay in the west to the Black Mountains in the east. It comprises a 150–450-m-thick (Allen 1974) sand-dominated sequence of fluvial and fluvio-lacustrine origin, which is distinguished from the sediments of the underlying Red Marls and overlying Brownstones by its primarily grey-green coloration, diagnostic macroflora and dispersed-miospore assemblages, and distinctive lithofacies associations.

Whilst the important Senni Beds Formation macroflora has been, and is still being, intensively studied, comparatively little is known about the sedimentology and provenance of the Formation. The most recent general account of the lithostratigraphy and sedimentology of the Senni Beds is contained in Allen's (1974) review of the Devonian rocks of Wales and the Welsh Borderland. To date, no detailed interpretations of the depositional environment(s) represented by the Senni Beds Formation have been published.

In central south Wales, where it attains a thickness of 300–380 m (Dineley and Williams 1978, fig. 31), the Senni Beds Formation consists of intraformational conglomerates (many of which are calcified) plus subordinate extraformational conglomerates, coarse to very fine grained sandstones, coarse to fine grained siltstones, some claystones, and occasional poorly developed calcretes. Whilst these lithologies are often rhythmically arranged (as, for example, in fining-upward cyclothems of variable complexity and completeness) there are many Senni Beds Formation sections, including that at Heol Senni Quarry, in which no over-all 'cyclic' organization of the constituent lithofacies units is discernible.

We interpret the Senni Beds Formation sequence of the Brecon Beacons area as having been deposited by a comparatively high discharge, mixed-load (but sand dominated), braided stream complex. Relatively high sedimentation rates and water-table levels during accumulation of the Senni Beds are indicated by the combination of the vertical succession of lithofacies units and the prevalence of grey-green colours within the Formation, plus the suites of stratification types and other sedimentary structures it contains.

In-channel and extra-channel sequences have been identified. In-channel facies recognized include: channel lags; channel-fill deposits; units formed by the migration of linguoid, transverse, lateral and ?rhomboid mid-channel bars, and low amplitude sand waves; bar delta wedges; and bar top sequences. Thick, multistorey sand bodies containing interbeds and/or lenses of intraformational conglomerate that overlie basal erosion surfaces imply repeated channel superimposition, filling and re-excavation. Many channel sand units are draped by thin mudstones deposited from suspension during waning flood stages. Local, comparatively rapid, channel shifting and consequent complete or partial channel abandonment, was common. Ponding of floodwaters occurred in channel cut-offs and (between flood stages) in parts of the secondary and tertiary distributaries of the active channel network. This local ponding, combined with decomposition of plant material (with the subsequent lowering of redox potentials), plus the presence of reworked calcrete glaebules and calcitized plant fragments (high pH and bicarbonate ion concentrations) resulted in the calcification of many channel-lag intraformational conglomerates.

Extra-channel and floodplain deposits of the Senni Beds Formation comprise proximal and distal crevasse splay sediments, some possible levee sediments, and thin, fine-grained, fluviolacustrine units laid down in temporary floodplain lakes. Sandstones interbedded with these mudstone-dominated fluviolacustrine units are thought to represent incursions of crevasse-splay sands deposited during major avulsion episodes. The Heol Senni pteraspidid may well have been carried from its habitat within the main channel system and deposited within a floodplain lake or channel-fill mud unit during one such flood event. Strongly reducing post-depositional conditions are indicated for the majority of these fluviolacustrine sediments by their typically blue-grey to grey-green coloration, and the preservation within them of pyrite nodules, macroplant cuticles, and miospores.

Vascular plants fourished along the shores of the temporary floodplain lakes, and colonized abandoned-channel fills and near-channel overbank deposits. High sedimentation rates and water-table levels, plus post-burial reducing conditions meant that the potential for preservation of these plants was comparatively good.

In the Brecon Beacons the Senni Beds Formation: Brownstones boundary has been drawn at the junction between the predominantly grey-green coloured sequence and the overlying red-brown succession, even though there are no major sedimentological differences between the lithofacies immediately below and above the contact. However, the Brownstones higher in the succession were laid down by sandy braided streams of a more shallow and ephemeral nature than those which deposited the Senni Beds.

The Senni Beds Formation is the lateral litho- and chronostratigraphic equivalent of the lower and middle portions of the 540–600-m-thick Mill Bay Formation (Cosheston Group) of south-west Dyfed, which Thomas (1978*a*, *b*) interpreted as the deposits of a braided-meandering river system (cf. Shelton and Noble 1974).

STRATIGRAPHY

The Senni Beds, together with the Brownstones of central south Wales, constitute the Breconian, one of four Stages into which the Old Red Sandstone of the Anglo-Welsh area has been subdivided. The stages, in ascending order, are the Downtonian, Dittonian, and Breconian of the Lower Old Red Sandstone, which are unconformably overlain by the Farlovian of the Upper Old Red Sandstone. The foundations of this classification were laid by King (1925, 1934) who, using a combination of faunal (mainly ostracoderms) and lithostratigraphic evidence, recognized four discrete 'series' or 'divisions' in the Old Red Sandstone of Shropshire. These were, (1) Downtonian (or Anaspida Marls),

(II) Dittonian (or *Pteraspis* cornstones) followed by a group of 'false-bedded brown sandstones' which King (equating them with the Black Mountains sequence) termed (III) the 'Brownstones'. Together these comprised the Lower Old Red Sandstone, and were succeeded unconformably by (IV) the Farlow Sandstones (-Farlovian Stage of King 1934) of Upper Old Red Sandstone age. Although retained at formation level, the term 'Brownstones' is now no longer used *sensu* King (1925). Instead, the stage-name Breconian was proposed by Croft (1953) to circumscribe the highest Lower Old Red Sandstone of the Anglo-Welsh Basin, namely that part 'lying between the Dittonian and Farlovian Stages' of King (1934).

Attention has already been drawn to the difficulties of interpreting the Breconian Stage division, and to the possibility of its overlap with the preceding Dittonian Stage (Allen *et al.* 1968; Allen 1974). These difficulties arise essentially because the Downtonian and Dittonian Stages are defined on a largely biostratigraphical basis in the vertebrate-rich succession of the Clee Hills, whilst the Breconian Stage is defined on a largely lithostratigraphical basis in the Brecon Beacons where vertebrates are extremely rare. As a consequence, the Dittonian–Breconian boundary has never been satisfactorily fixed.

In the Clee Hills, refinement of King's (1925, 1934) original vertebrate stratigraphy by White (1950, 1961) and Ball and Dineley (1952, 1961) has resulted in the recognition of a number of ostracoderm zones which have proved to be of some value in correlation (White 1950, 1956). The Dittonian is characterized by its pteraspid faunas, the highest zone being that of *A. leachi* which is some 183 m (600 feet) thick (Ball and Dineley 1961), but which terminates well below the top of beds which are assigned on lithological grounds to the Dittonian Series (Ball and Dineley 1961). Biostratigraphically, the Dittonian Stage is 'regarded as being terminated by the appearance of *Rhinopteraspis cornubica*' (Allen *et al.* 1968). However, although *R. cornubica* (McCoy) (syn. *R. dunensis* (Roemer)) has come to be accepted as the 'Breconian zonal fossil' (Allen 1974), it has not yet been recorded from the Clee Hills and, in the whole of the south Wales Breconian, appears to be restricted to a single locality. This lack of evidence makes it impossible to determine the precise position of a faunal boundary between the *A. leachi* and *R. cornubica* zones. While it was long assumed that such a boundary would correspond to lithostratigraphical divisions, the discovery that the pteraspid from the Brownstones of Mitcheldean was *A. leachi* and not *R. cornubica* (Allen *et al.* 1968) demonstrated that this was not so.

In the Brecon Beacons, the Breconian Stage, as envisaged by Croft (1953), is characterized by its abundant and distinctive macroflora which includes *Drepanophycus* and *Gosslingia*, and by the presence of *R. cornubica*. Its junction with the Dittonian is drawn at a colour change (Allen 1974) in an area where ostracoderms are very rare. The flora occurs at many localities within the Senni Beds but the Brownstones appear to be unfossiliferous. The one locality at which *R. cornubica* has been found is a quarry high up in the Senni Beds, which are there in the region of 300 m (1000 feet) thick. This level would seem to be substantially above the highest appearance of *A. leachi* in the Clee Hills (Allen 1974). The macroflora of the Senni Beds, although probably the most extensive and representative Lower Old Red Sandstone flora in Britain, is of little stratigraphic value. The Breconian plants are relatively scarce and their distribution is facies controlled. Furthermore, owing to the lack of faunal control, it must be considered as a distinct possibility that they are Dittonian in age in terms of the ostracoderm zones.

THE STRATIGRAPHIC SIGNIFICANCE OF THE HEOL SENNI PTERASPIDID

The discovery of pteraspidid material in association with a typical Breconian macroflora, and datable on the basis of a dispersed miospore assemblage, is a significant contribution toward resolving the dubious status of the Breconian Stage division. Unfortunately, the pteraspidid from Heol Senni cannot be referred either to *R. cornubica* or to *A. leachi*; it is a distinct species of *Althaspis*, showing similarities to forms from Podolia and France, as well as to the British species. It does, however, provide some support for the view that there is overlap between the Dittonian and Breconian Stages.

The fact that *A. senniensis* is smaller, and has a less attenuated rostrum than *A. leachi*, does suggest that it is more primitive. While this alone is insufficent evidence to suggest that it occurs at a lower stratigraphic level, it is relevant to note the stratigraphic distribution of other species of *Althaspis*. The rather similar *A. vimiensis* White, from Belgium (White 1960; Blieck 1977), there occurs only 17 metres above *Belgicaspis crouchi*; the latter is the characteristic pteraspidid of the zone immediately preceding that of *A. leachi* in Britain. The stratigraphic distribution of the species described by Stensiö (1958, 1964) was not given, but the range of *A. samsonowiczi* Tarlo (syn. *A. elongata* (Zych)) overlaps with that of *B. crouchi* in the Old Red Group of Podolia (Obruchev and Talimaa, 1967). In Spitsbergen, *A. anatirostra* Blieck is found at a level correlated with the base of the *B. crouchi* or top of the *Protopteraspis leathensis* zone of the Dittonian (Goujet and Blieck 1977).

Thus *A. senniensis* can be considered to be a pteraspidid of Dittonian aspect. Its presence in the Senni Beds indicates overlap between the Dittonian and Breconian Stages, as currently defined, but the extent of this overlap remains uncertain. In view of the scarcity of ostracoderms at this level in the Lower Old Red Sandstone, it seems unlikely that they, alone, will ever be of use in resolving the problem of the Dittonian–Breconian boundary; the eventual solution must involve choosing other organisms for zonal purposes. Work by Mortimer (1967), Chaloner and Streel (1968) and Richardson and Lister (1969) has drawn attention to the great potential of dispersed miospore assemblages for use in relative age determinations and stratigraphic correlations within the Anglo-Welsh Lower Old Red Sandstone. Thomas (1978*a*) has already used such assemblages to correlate between the Breconian of Pembrokeshire and Breconshire; it seems probable that they could eventually be used to define the Dittonian-Breconian junction.

In view of this, the discovery of a diverse, well-preserved and distinctive miospore assemblage, in association with an ostracoderm, is of great stratigraphic significance. It is noteworthy that the mid Middle to lower Upper Siegenian age of the Senni Beds Formation, as deduced from the miospore assemblage (Thomas 1978*b*), agrees well with the Middle to Upper Siegenian age suggested by White (1956) on the basis of *R. cornubica*, and is supported by Richardson and Rasul's (1979) comparison with the Apley Barn Borehole.

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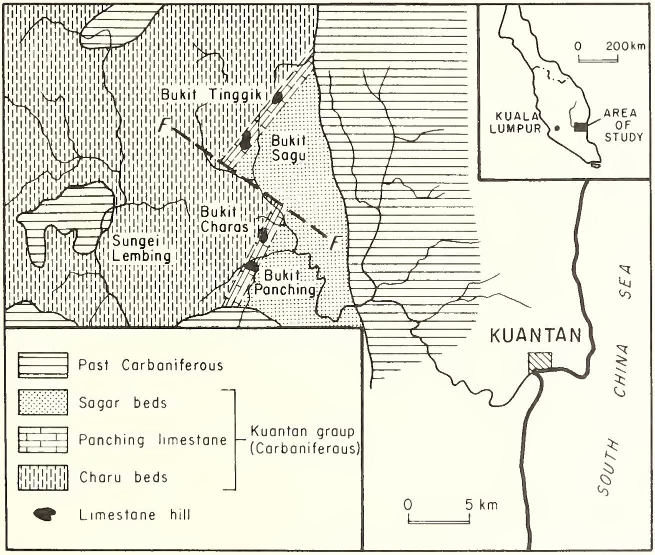
UPPER CARBONIFEROUS CONODONT FAUNAS OF THE PANCHING LIMESTONE, PAHANG, WEST MALAYSIA

by I. METCALFE

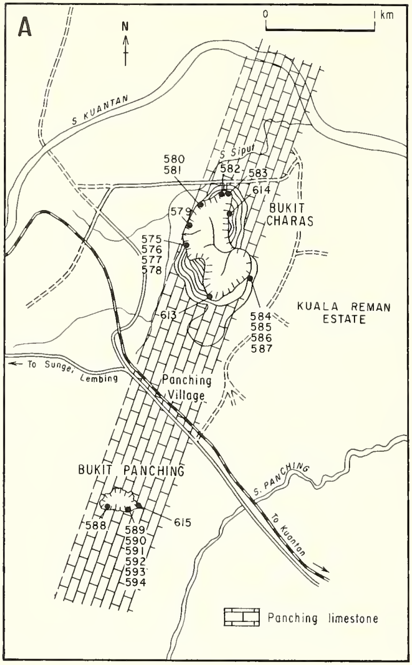
ABSTRACT. The Panching limestone, from Pahang, West Malaysia, has yielded a rich conodont fauna which represents the *Idiognathoides noduliferus–Streptognathodus lateralis* conodont Zone. Two subzones are recognized for the Panching limestone, a lower *Idiognathoides noduliferus inaequalis–Gnathodus commutatus* Subzone and an upper *Idiognathoides noduliferus japonicus–Rhachistognathus* Subzone. The age of the faunas in terms of European Stages is Chokierian (H_1) and possibly Alportian (H_2). It is considered that the Mississippian–Pennsylvanian boundary may be correlated with a level in the Panching limestone.

THE Panching limestone (a term here used informally pending formal designation; Metcalfe, Idris, and Tan, in prep.) crops out as a narrow band running SSW.–NNE. in the Panching area approximately twenty miles north-west of Kuantan, Pahang, West Malaysia (text-fig. 1). The



TEXT-FIG. 1. Sketch-map of the area west of Kuantan, Pahang, West Malaysia, showing the location of the Panching limestone.

[Palaeontology, Vol. 23, Part 2, 1980, pp. 297–314, pls. 37–38.]



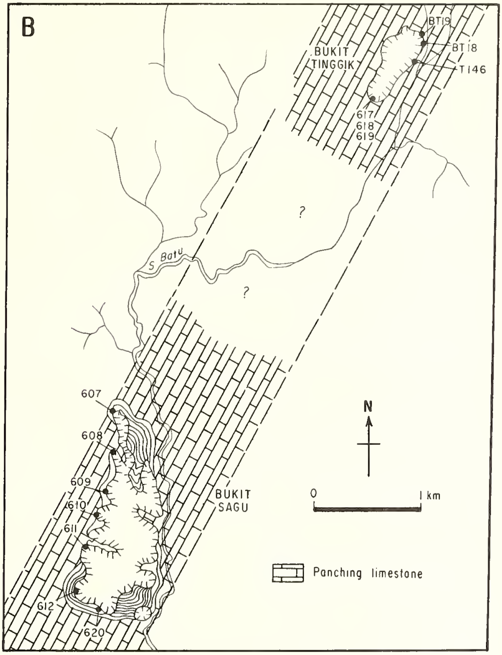
TEXT-FIG. 2A. Sketch-map showing sample localities at Bukit Panching and Bukit Charas.

limestone, which is 600 m thick, conformably overlies a series of alternating shales and sandstones approximately 1500 m thick, here referred to as Charu beds, and is overlain by alternating conglomerates, shales, and sandstones approximately 1600 m thick, here termed the Sagor beds. These sediments, which constitute the 'Kuantan Group' of Alexander (1959), generally dip steeply south-eastwards, but are tightly folded in many places.

Exposures of the Panching limestone, which is massive, fossiliferous, and partly recrystallized, occur as isolated limestone hills, which rise steeply out of relatively flat land to approximately 250 m. There are four limestone hills, which are from south to north, Bukit Panching, Bukit Charas, Bukit Sagu, and Bukit Tinggik. Samples were collected from each of the hills, and text-fig. 2 gives the locations of samples, which were all collected at ground level.

The age of the Panching limestone was originally regarded as Viséan (Muir-Wood *et al.* 1948; Fitch 1951; Sakagami 1972; Ozawa 1975). Igo and Koike (1968) and Mamet and Saurin (1970), however, described conodonts and foraminifera from Bukit Charas which they considered to be Namurian in age. Igo and Koike (1968) recorded *Idiognathoides noduliferus*, *Gnathodus bilineatus*, *Spathognathodus campbelli*, *Ozarkodina* sp., and *Hindeodella* sp. from Bukit Charas. The present study was undertaken to extract a more varied conodont fauna and to date the limestone more precisely in terms of conodont biostratigraphy.

TEXT-FIG. 2B. Sketch-map showing sample localities at Bukit Sagu and Bukit Tinggik.



SYSTEMATIC PALAEONTOLOGY

All figured specimens are deposited in the Department of Geology, University of Malaya.

Genus *Apatognathus* Branson and Mehl, 1934

Type species: *Apatognathus varians* Branson and Mehl, 1934

Apatognathus cuspidatus Varker

Plate 37, fig. 1

1967 *Apatognathus*? *cuspidata* Varker, p. 131, pl. 17, figs. 4, 6–10.
1970 *Apatognathus*? *cuspidatus* Varker; Reynolds, p. 7, pl. iii, fig. 4.

Remarks. The specimen is unfortunately broken but possesses the characteristic apical denticle of *A. cuspidatus*.

Material. 1 specimen, figured A339.

Apatognathus libratus Varker

Plate 37, fig. 4

1967 *Apatognathus*? *librata* Varker, p. 134, pl. 18, figs. 3, 6, 8, 9, 12, 13.
1969 *Apatognathus* cf. *libratus* Varker; Rhodes, Austin and Druce, p. 75, pl. 20, fig. 8*a*, *b*.
1970 *Apatognathus*? *libratus* Varker; Reynolds, p. 7, pl. iii, fig. 2.
1974 *Apatognathus libratus* Varker; Austin and Husri, pl. 10, fig. 6*a*, *b*.

Material. 1 specimen, figured A340.

Apatognathus scalenus Varker

Plate 37, fig. 2

1967 *Apatognathus*? *scalena* Varker, p. 136, pl. 18, figs. 1, 2, 4, 5.
1969 *Apatognathus scalenus* Varker; Rhodes, Austin and Druce, p. 74, pl. 20, figs. 9*a*–11*b* (with synonomy).
1970 *Apatognathus*? *scalenus* Varker; Reynolds, p. 7, pl. iii, fig. 6.
1974 *Apatognathus scalenus* Varker; Austin and Husri, pl. 10, fig. 12*a*, *b*.

Remarks. The present specimen has a more pronounced inward curvature of the apical denticle than is normal in *A. scalenus*, but this is not considered of specific significance.

Material. 1 specimen, figured A341.

Genus *Geniculatus* Hass, 1953

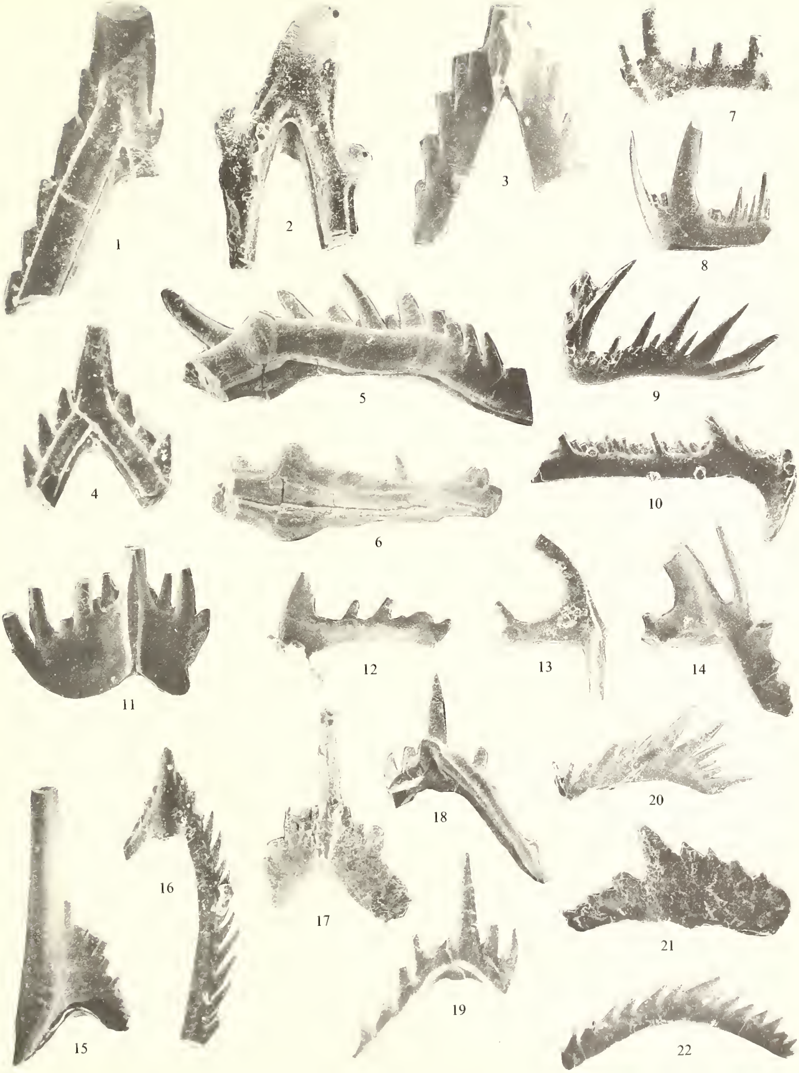
Type species: *Polygnathus*? *claviger* Roundy, 1926

EXPLANATION OF PLATE 37

All figures are scanning electron micrographs.

Fig. 1. *Apatognathus cuspidatus* Varker, inner lateral view of A339, sample 579, × 120.
Fig. 2. *Apatognathus scalenus* Varker, inner lateral view of A341, sample 614, × 100.
Fig. 3. *Hibbardella acuta* Murray and Chronic, posterior view of A352, sample 588, × 100.
Fig. 4. *Apatognathus libratus* Varker, inner lateral view of A340, sample 579, × 120.
Figs. 5, 6. *Geniculatus claviger* (Roundy). 5. inner lateral view of A342, sample 588, × 100. 6. aboral view of A342, × 100.
Fig. 7. *Hindeodella undata* Branson and Mehl, lateral view of A355, sample 588, × 60.
Fig. 8. *Hindeodella mehli* Elias, lateral view of A356, sample 588, × 60.
Fig. 9. *Hindeodella uncata* Hass, oral view of A357, sample 610, × 100.
Fig. 10. *Hindeodella ibergensis* Bischoff, lateral view of A384, sample 585, × 100.
Fig. 11. *Hibbardella pennata* Higgins, posterior view of A353, sample 588, × 120.
Fig. 12. *Ligonodina roundyi* Hass, lateral view of A366, sample 588, × 60.
Figs. 13, 14. *Lonchodina bischoffi* Higgins and Bouckaert. 13. inner lateral view of A367, sample 588, × 60. 14. inner lateral view of A368, sample 588, × 50.
Fig. 15. *Neoprioniodus singularis* (Hass), inner lateral view of A370, sample 588, × 60.
Fig. 16. *Synprioniodina microdenta* Ellison, lateral view of A381, sample 585, × 100.
Fig. 17. *Hibbardella geniculata* Higgins, posterior view of A354, sample 578, × 100.
Figs. 18, 19. *Lonchodina ponderosa* Ellison. 18. aboral view of A369, sample 580, × 50. 19. oral view of A369.
Fig. 20. *Subbryantodus subaequalis* Higgins, lateral view of A380, sample 588, × 60.
Fig. 21. *Ozarkodina* sp., lateral view of A373, sample 578, × 100.
Fig. 22. *Ozarkodina delicatula* (Stauffer and Plummer), lateral view of A371, sample 579, × 50.

PLATE 37



METCALFE, Carboniferous conodonts

Geniculatus claviger (Roundy)

Plate 37, figs. 5, 6

1926 *Polygnathus*? *claviger* Roundy, p. 14, pl. 4, figs. 1*a–c*, 2*a–b*.
1926 *Prioniodus* sp. D Roundy (partim), p. 11, pl. 4, fig. 13*a–b*.
1926 *Prioniodus healdi* Roundy, p. 10, pl. 4, fig. 5*a–b*.
1975 *Geniculatus claviger* (Roundy) Higgins, p. 27, pl. 2, fig. 5 (with synonomy).

Material. 4 specimens, figured A342.

Genus *Gnathodus* Pander, 1856

Type species: *Gnathodus mosquensis* Pander, 1856

Gnathodus bilineatus (Roundy)

Plate 38, figs. 5, 8, 9

1926 *Polygnathus bilineatus* Roundy, p. 13, pl. 3, fig. 10*a–c*.
1974 *Gnathodus bilineatus* (Roundy) Lane and Straka, pp. 72–77, fig. 32: 1–5, 7, 9, 11–13; fig. 33: 11–13, 19–23, 25, 28–32; fig. 34: 10, 13–26; fig. 40: 27 (with synonomy).
1975 *Gnathodus bilineatus bilineatus* (Roundy) Higgins, p. 28, pl. 11, figs. 1–4, 6, 7 (with synonomy).
1975 *Gnathodus bilineatus bollandensis* Higgins and Bouckaert; Higgins, p. 29, pl. 11, figs. 5, 8–13 (with synonomy).

Material. 18 specimens, figured A343, A344, A345.

EXPLANATION OF PLATE 38

All figures are scanning electron micrographs.

Fig. 1. *Gnathodus girtyi simplex* Dunn, oral view of A350, sample 610, × 50.

Fig. 2. *Gnathodus nodosus* (Bischoff), oral view of A351, sample 577, × 50.

Figs. 3, 4. *Gnathodus commutatus* (Branson and Mehl). 3. oral view of A347, sample 588, × 60. 4. oral view of A346, sample 588, × 50.

Figs. 5, 8, 9. *Gnathodus bilineatus* (Roundy). 5. oral view of A344, sample 575, × 100. 8. oral view of A343, sample 575, × 100. 9. oral view of A345, sample 580, × 120.

Fig. 6. *Gnathodus girtyi rhodesi* Higgins, oral view of A349, sample 578, × 160.

Fig. 7. *Spathognathodus scitulus* (Hinde), lateral view of A375, sample 579, × 100.

Figs. 10, 11, 12, 15. *Idiognathoides noduliferus inaequalis* Higgins. 10. oral view of A360, sample 610, × 50. 11. oral view of A358, sample 618, × 100. 12. oral view of A361, sample 585, × 50. 15. oral view of A359, sample 620, × 50.

Fig. 13. *Spathognathodus campbelli* Rexroad, lateral view of A374, sample 579, × 100.

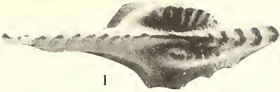
Figs. 14, 17. *Idiognathoides noduliferus japonicus*. 14, oral view of A363, sample 586, × 50. 17. oral view of A362, sample 586, × 100.

Figs. 16, 18. *Idiognathoides noduliferus noduliferus* (Ellison and Graves). 16. oral view of A364, sample 585, × 50. 18. oral view of A365, sample 585, × 50.

Figs. 19–22. *Streptognathodus lateralis* Higgins and Bouckaert. 19. oral view of A379, sample 617, × 25. 20. oral view of A377, sample 620, × 50. 21. oblique oral view of A378, sample 618, × 50. 22. oral view of A376, sample 620, × 50.

Fig. 23. *Rhachistognathus primus* Dunn, oral view of A383, sample 585, × 100.

Figs. 24, 25. *Rhachistognathus muricatus* (Dunn). 24. oral view of A382, sample 620, × 50. 25. outer lateral view of A382.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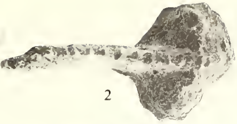
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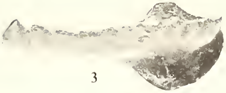
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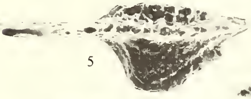
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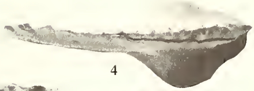
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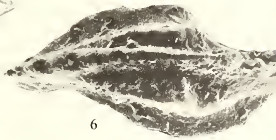
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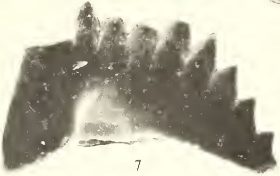
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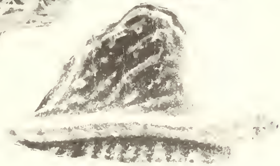
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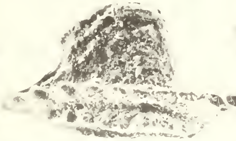
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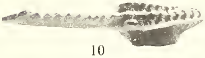
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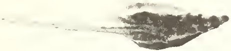
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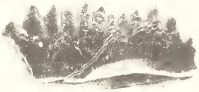
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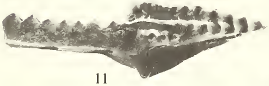
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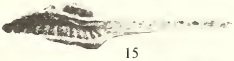
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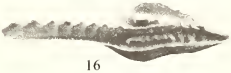
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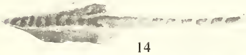
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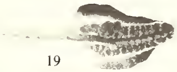
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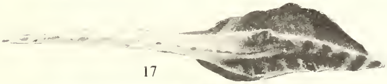
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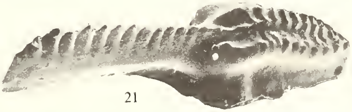
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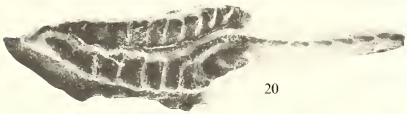
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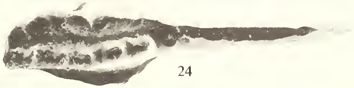
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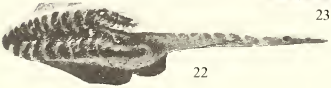
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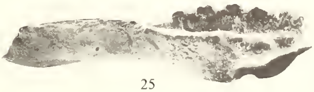
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METCALFE, Carboniferous conodonts

Gnathodus commutatus (Branson and Mehl)

Plate 38, figs. 3, 4

1941 *Spathognathodus commutatus* Branson and Mehl, p. 98, pl. 19, figs. 1–4.
1975 *Paragnathodus commutatus* (Branson and Mehl) Higgins, p. 70, pl. 7, figs. 7–9, 11, 13, 16, 20, 21 (with synonomy).

Material. 21 specimens, figured A346, A347.

Gnathodus girtyi rhodesi Higgins

Plate 38, fig. 6

1975 *Gnathodus girtyi rhodesi* Higgins, p. 32, pl. 10, figs. 3, 4 (with synonomy).

Material. 3 specimens, figured A349.

Gnathodus girtyi simplex Dunn

Plate 38, fig. 1

1965 *Gnathodus girtyi simplex* Dunn, p. 1158, pl. 140, figs. 2, 3, 12.
1975 *Gnathodus girtyi simplex* Dunn; Higgins, p. 33, pl. 10, figs. 3, 4 (with synonomy).

Remarks. G. girtyi simplex has been recorded from the Mississippian and basal Pennsylvanian of the U.S.A. (Lane and Straka 1974) and from the Pendleian and Arnsbergian Stages of Britain (Higgins 1975). This subspecies was considered by Dunn (1970*a*) to be the ancestor of *Idiognathoides noduliferus*.

Material. 2 specimens, figured A350.

Gnathodus nodosus (Bischoff)

Plate 38, fig. 2

1957 *Gnathodus commutatus nodosus* Bischoff, p. 23, pl. 4, figs. 12, 13.
1960 *Gnathodus cruciformis* Clarke, p. 25, pl. iv, figs. 10–12.
1969 *Gnathodus mononodosus* Rhodes, Austin and Druce, p. 103, pl. 19, figs. 13*a*–15*d*.
1975 *Paragnathodus cruciformis* (Clarke) Higgins, p. 71, pl. 7, fig. 10.
1975 *Paragnathodus mononodosus* (Rhodes, Austin and Druce) Higgins, p. 71, pl. 7, fig. 14 (with synonomy).
1975 *Paragnathodus nodosus* (Bischoff) Higgins, p. 72, pl. 7, figs. 12, 15, 17–19, 22, 23 (with synonomy).

Material. 3 specimens, figured A351.

Genus *Hibbardella* Ulrich and Bassler

Type species: *Prioniodus angulatus* Hinde, 1879

Hibbardella acuta Murray and Chronic

Plate 37, fig. 3

For synonomy and description see Higgins (1975, p. 34).

Material. 4 specimens, figured A352.

Hibbardella geniculata Higgins

Plate 37, fig. 17

1975 *Hibbardella geniculata* Higgins, p. 35, pl. 6, figs. 11, 12, 14.

Material. 1 specimen, figured A354.

Hibbardella pennata Higgins

Plate 37, fig. 11

For synonomy see Higgins (1975, p. 36) and description Higgins (1961, p. 213).

Material. 6 specimens, figured A353.

Genus *Hindeodella* Ulrich and Bassler, 1926

Type species: *Hindeodella subtilis* Ulrich and Bassler, 1926

Hindeodella ibergensis Bischoff

Plate 37, fig. 10

For synonomy see Higgins (1975, p. 38).

Material. 18 specimens, figured A384.

Hindeodella mehli Elias

Plate 37, fig. 8

1942 *Lochreia montanaensis* Scott (partim), pl. 39, fig. 7; pl. 40, fig. 18.
1956 *Hindeodella bigeniculata* Elias (partim), p. 106, pl. 1, figs. 20, 21.
1956 *Hindeodella mehli* Elias, p. 108, pl. 1, figs. 22–24.
1957 *Hindeodella germana* Holmes; Bischoff (partim), p. 27, pl. 6, fig. 32.
1958 *Hindeodella montanaensis* (Scott) Stanley (partim), p. 465, pl. 64, figs. 1–5.
1961 *Hindeodella germana* Holmes; Higgins (partim), pl. 10, fig. 12.
1968 *Hindeodella germana* Holmes; Higgins and Bouckaert, p. 36, pl. 1, fig. 12.
1969 *Hindeodella montanaensis* (Scott) Rhodes, Austin and Druce, p. 123, pl. 28, figs. 21, 26.
1974 *Hindeodella montanaensis* (Scott) Austin and Husri, pl. 15, fig. 16.
1975 *Hindeodella germana* Holmes; Higgins, p. 38, pl. 5, fig. 6.

Remarks. Scott (1942) described this form species as part of the multi-element species *Lochrea montanaensis*. It is considered inappropriate to use the multi-element specific name for the form species, and therefore the next unambiguous name available (i.e. *H. mehli* Elias, 1956) is used.

Material. 3 specimens, figured A356.

Hindeodella uncata Hass

Plate 37, fig. 9

For synonomy see Higgins (1975, p. 44).

Material. 1 specimen, figured A357.

Hindeodella undata Branson and Mehl

Plate 37, fig. 7

For synonomy see Higgins (1975, p. 44).

Material. 1 specimen, figured A355.

Genus *Idiognathoides* Harris and Hollingsworth, 1933

Type species: *Idiognathoides sinuatus* Harris and Hollingsworth, 1933

Idiognathoides noduliferus Group

In this paper, the subdivision of *I. noduliferus* into three subspecies, *I. noduliferus inaequalis*, *I. noduliferus noduliferus*, and *I. noduliferus japonicus* made by Higgins (1975) is followed. Higgins (1975, p. 52) showed that these three subspecies form a transition series by reduction of the outer lateral platform.

Idiognathoides noduliferus inaequalis Higgins

Plate 38, figs. 10, 11, 12, 15

1975 *Idiognathoides noduliferus inaequalis* Higgins, p. 53, pl. 12, figs. 1–7, 12; pl. 14, figs. 11–13; pl. 15, figs. 10, 14.

Remarks. This subspecies is recognized by having four or more nodes developed on the outer platform.

Material. 211 specimens, figured A358–A361.

Idiognathoides noduliferus japonicus (Igo and Koike)

Plate 38, figs. 14, 17

1964 *Streptognathodus japonicus* Igo and Koike, p. 188, pl. 28, figs. 5–10.
1975 *Idiognathoides noduliferus japonicus* (Igo and Koike) Higgins, p. 54, pl. 14, figs. 7–10 (with synonomy).

Remarks. This subspecies is characterized by having only a single node on its outer platform.

Material. 13 specimens, figured A362, A363.

Idiognathoides noduliferus noduliferus (Ellison and Graves)

Plate 38, figs. 16, 18

1941 *Cavusgnathus noduliferus* Ellison and Graves, p. 4, pl. 3, fig. 4.
1974 *Idiognathoides noduliferus* (Ellison and Graves) Lane and Straka, p. 85, fig. 35: 1–15, fig. 41: 15–17.
1975 *Idiognathoides noduliferus noduliferus* (Ellison and Graves) Higgins, p. 54, pl. 14, figs. 15, 16 (with synonomy).

Remarks. This subspecies is characterized by having two or three nodes developed on its outer platform.

Material. 75 specimens, figured A364, A365.

Genus *Ligonodina* Ulrich and Bassler, 1926

Type species: *Ligonodina pectinata* Ulrich and Bassler 1926

Ligonodina roundyi Hass

Plate 37, fig. 12

For synonomy see Higgins (1975, p. 58).

Material. 1 specimen, figured A366.

Genus *Lonchodina* Ulrich and Bassler, 1926

Type species: *Lonchodina typicalis* Ulrich and Bassler, 1926

Lonchodina bischoffi Higgins and Bouckaert

Plate 37, figs. 13, 14

1968 *Lonchodina bischoffi* Higgins and Bouckaert, p. 43.
1975 *Lonchodina bischoffi* Higgins and Bouckaert; Higgins, p. 59, pl. 2, figs. 1–4, 8 (with synonomy).

Material. 3 specimens, figured A367, A368.

Lonchodina ponderosa Ellison

Plate 38, figs. 18, 19

1941 *Lonchodina*? *ponderosa* Ellison, p. 116, pl. 20, figs. 37–39.
1975 *Lonchodina ponderosa* Ellison; Higgins, p. 60, pl. 2, fig. 11 (with description).

Material. 1 specimen, figured A369.

Genus *Neoprioniodus* Rhodes and Muller, 1956

Type species: *Prioniodus conjunctus* Gunnell, 1931

Neoprioniodus scitulus? (Branson and Mehl)

For synonomy see Rhodes, Austin and Druce (1969, p. 162).

Material. 2 fragmentary specimens.

Neoprioniodus singularis (Hass)

Plate 37, fig. 15

For synonomy see Thompson (1972, p. 37).

Material. 10 specimens, figured A370.

Genus *Ozarkodina* Branson and Mehl, 1933

Type species: *Ozarkodina typica* Branson and Mehl, 1933

Ozarkodina delicatula (Stauffer and Plummer)

Plate 37, fig. 22

For synonomy see Webster (1969) and Higgins (1975).

Material. 33 specimens, figured A371.

Ozarkodina sp.

Plate 37, fig. 21

Remarks. The specimen illustrated resembles young forms of *O. delicatula* but is considered to be too large for a juvenile of that species.

Material. 1 specimen, figured A373.

Genus *Rhachistognathus* Dunn, 1966

Type species: *Rhachistognathus primus* Dunn, 1966

Rhachistognathus muricatus (Dunn)

Plate 38, figs. 24, 25

1965 *Cavusgnathus muricatus* Dunn, p. 1147, pl. 140, figs. 1, 4.
1974 *Rhachistognathus muricatus* (Dunn) Lane and Straka, p. 97, fig. 35: 16, 17, 24, 30, 31 (with synonomy).

Remarks. This species is similar to *Idiognathoides minutus* Higgins and Bouckaert, but Higgins (1975, p. 50) has pointed out that *I. minutus* is normally half the size of *R. muricatus*, and does not possess the medial row of nodes developed posteriorly in many specimens of *R. muricatus*.

Material. 3 specimens, figured A382.

Rhachistognathus primus Dunn

Plate 38, fig. 23

1966 *Rhachistognathus prima* Dunn, p. 1301, pl. 157, figs. 1, 2.
1974 *Rhachistognathus primus* Dunn; Lane and Straka, p. 98, fig. 35: 18–23, 25–29, 32–40, fig. 44: 6 (with synonomy).

Remarks. Lane and Straka (1974) have shown that *R. muricatus* and *R. primus* are intergradational via a transitional morphotype *R. transitorius*.

Material. 1 specimen, figured A383.

Genus *Spathognathodus* Branson and Mehl, 1941

Type species: *Ctenognathus murchisoni* Pander, 1856.

Spathognathodus campbelli Rexroad

Plate 38, fig. 13

1957 *Spathognathodus campbelli* Rexroad, p. 37, pl. 3, figs. 13–15.
1975 *Spathognathodus campbelli* Rexroad; Higgins, p. 73, pl. 10, fig. 11 (with synonomy).

Remarks. This is a somewhat variable species. The denticles of the unit may be sub-equal or may be larger in the anterior half. The lateral oral outline may be straight, or in some specimens considerably convex. In oral view the unit varies from straight to bowed.

Material. 7 specimens, figured A374.

Genus *Streptognathodus* Stauffer and Plummer, 1932

Type species: *Streptognathodus exelsus* Stauffer and Plummer, 1932.

Streptognathodus lateralis Higgins and Bouckaert

Plate 38, figs. 19–22

1968 *Streptognathodus lateralis* Higgins and Bouckaert, p. 45, pl. 5, figs. 1–4, 7.
1975 *Streptognathodus lateralis* Higgins and Bouckaert; Higgins, p. 73, pl. 12, fig. 9; pl. 17, figs. 10, 11, 13, 14 (with synonymy).

Material. 25 specimens, figured A376–A379.

Genus *Subbryantodus* Branson and Mehl, 1934

Type species: *Subbryantodus arcuatus* Branson and Mehl, 1934.

Subbryantodus subaequalis Higgins

Plate 37, fig. 20

For synonymy see Higgins (1975, p. 74) and description Higgins (1961, p. 218).

Material. 4 specimens, figured A380.

Genus *Synprioniodina* Ulrich and Bassler, 1926

Type species: *Synprioniodina alternata* Ulrich and Bassler, 1926

Synprioniodina microdenta Ellison

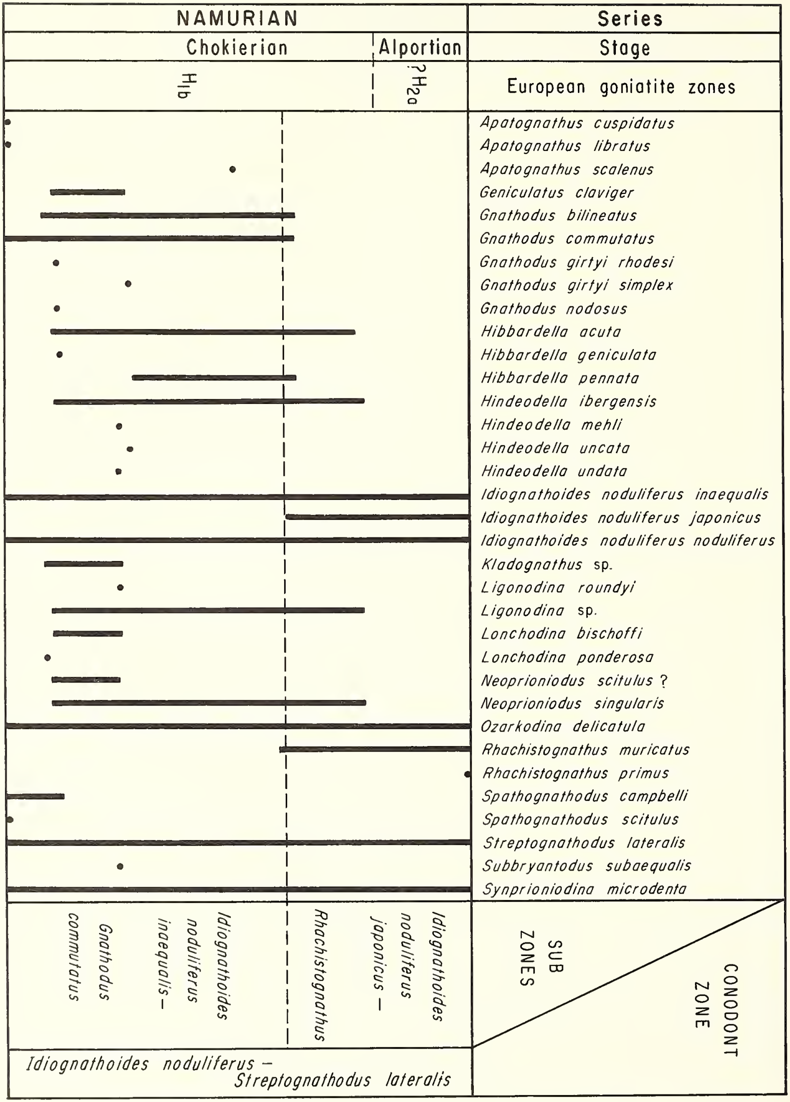
Plate 37, fig. 16

For synonymy and description see Higgins (1975, p. 75).

Material. 8 specimens, figured A381.

CONODONT ZONATION

The ranges of conodont species in the Panching limestone are given in text-fig. 3 and the numerical distribution in individual samples in Table 1. The Panching limestone fauna contains an assemblage characteristic of Higgins's (1975) *Idiognathoides noduliferous* Subzone and is therefore referred to the *I. noduliferus–Streptognathodus lateralis* Zone. In the Panching limestone, a lower and an upper fauna are recognized and these are here designated subzones. The lower subzone, the *I. noduliferus inaequalis–Gnathodus commutatus* Subzone, is taken to have its lower limit defined by the first appearance of *I. noduliferus inaequalis* and or *I. noduliferus noduliferus* and its upper limit defined as the first appearance of *I. noduliferus japonicus*. This subzone is characterized by an association of gnathodids and idiognathoidids, and in particular an association of *G. bilineatus*, *I. noduliferus inaequalis*, *I. noduliferus noduliferus*, and *G. commutatus*. The upper subzone, the *I. noduliferus*



TEXT-FIG. 3. Ranges of conodont species in the Panching limestone.

TABLE 1. Numerical distribution of conodont species in individual samples from the Panching limestone. Samples are only in stratigraphic order for each individual hill.

LIMESTONE HILL	SAMPLE NUMBER	Apatognathus cuspidatus	Apatognathus libratus	Apatognathus scalenus	Apatognathus sp	Geniculatus claviger	Gnathodus bilineatus	Gnathodus commutatus	Gnathodus girtyi rhodesi	Gnathodus girtyi simplex	Gnathodus nodosus	Hibbardella acuta	Hibbardella geniculata	Hibbardella pennata	Hibbardella sp	Hindeodella ibergensis	Hindeodella mehli	Hindeodella uncata	Hindeodella undata	Hindeodella sp	Idiognathoides noduliferus inaequalis	Idiognathoides noduliferus japonicus	Idiognathoides noduliferus noduliferus	Idiognathoides ? sp	Kladognathus sp	Ligonodina roundyi	Ligonodina sp	Lonchodina bischoffi	Lonchodina ponderosa	Lonchodina sp	Neoprioniodus scitulus	Neoprioniodus singularis	Neoprioniodus sp	Ozarkodina delicatula	Ozarkodina sp	Rhachistognathus muricatus	Rhachistognathus primus	Spathognathodus campbelli	Spathognathodus scitulus	Spathognathodus sp	Streptognathodus lateralis	Streptognathodus ? sp	Subbryantodus subaequalis	Synprioniodina microdenta	Synprioniodina sp	Gen indet	Total	Sample weight in kilograms	Concentration of conodonts in spec/kg
BUKIT TINGGIK	T146															2				6	11						1					1		1	2					1	1					11	37	2.0	18
	8T18											1								1	3																				1					2	8	2.0	4
	8T19														1					1	3		4											1							2					11	23	2.5	9
	619																			2	4		1												1											3	11	2.0	5
	618							1												11	12		5											1	3						3			1		19	56	2.0	28
	617						1							1		2				14	34	3	6											8	1						2					30	102	3.0	34
BUKIT SAGU	620															3				4	29		11											1	1	1					2					21	73	2.0	37
	612																			1																										2	3	2.0	1.5
	611														1					8	2																			1						3	15	2.0	8
	610							4		2				1		1		1		24	6									1		1		1										2		13	59	2.0	30
	609						1	1												17	6		3											1	2											7	38	2.0	19
	608																			2															1											1	4	2.0	2
	607																																														0	2.0	0
BUKIT CHARAS	587																			2		1		2																						5	10	2.0	5
	586																			8		6	7	1										2		1										5	30	4.0	7
	585															1				6	14	3	28	5										6	1	1	1				1			1		23	91	3.5	25
	584																																														0	2.0	0
	613																																													3	3	2.0	1.5
	614			1																																											1	2.0	0.5
	583																																														0	2.0	0
	582																			2																					1					6	9	2.0	4
	578				1			3	1		1		1			2				42	4		1				1	1			1	3		4	5			1			1			2		24	99	4.0	25
	577						1	3			2									1							1											1								8	18	3.5	5
	576																																														0	3.0	0
	575					2	14		2			2								29	31			6									2		10			4			4	2		1	2	56	167	7.0	24
	581																			1	3																									4	8	1.0	8
	580						2								1					7	17			1	1				1					1								1				17	50	6.0	8
	579	1	1					1												11	22		9	1										4				1	1		2			1		65	120	9.0	13
BUKIT PANCHING	615																																														0	2.0	0
	594																																													2	2	2.0	1
	593																																								1						1	2.0	0.5
	592																																														0	2.0	0
	591																																													4	4	2.0	2
	590																				1																									3	4	2.0	2
	589																																														0	2.0	0
	588					2		8				1		3		7	3		1	67	9				1	1	1	2			1	5		2	2						4		4			24	148	5.5	27

japonicus–Rhachistognathus Subzone, has its base at the first appearance of *I. noduliferus japonicus* and its upper limit taken at the first appearance of *I. corrugatus* and is characterized by an association of *I. noduliferus inaequalis*, *I. noduliferus noduliferus*, *I. noduliferus japonicus*, *R. muricatus* and *R. primus*.

Correlation with other areas

Namurian conodonts are known from Europe, Japan, North America, and Australia. The best-described successions of faunas are from Britain, Belgium, Japan, Nevada, Utah, Arkansas, and Oklahoma. The correlation of these faunas with the assemblages from the Panching limestone is shown in text-fig. 4 and discussed below.

Correlation with Europe. The sequence of Namurian conodont faunas in Europe is poorly known except in northern England, where Higgins (1975) has recognized seven zones and four subzones

TABLE 1. Numerical distribution of conodont species in individual samples from the Panching limestone. Samples are only in stratigraphic order for each individual hill.

LIMESTONE HILL	SAMPLE NUMBER	*Apatognathus cuspidatus*	*Apatognathus libratus*	*Apatognathus scalenus*	*Apatognathus* sp	*Geniculatus claviger*	*Gnathodus bilineatus*	*Gnathodus commutatus*	*Gnathodus girtyi rhodesi*	*Gnathodus girtyi simplex*	*Gnathodus nodosus*	*Hibbardella acuta*	*Hibbardella geniculata*	*Hibbardella pennata*	*Hibbardella* sp	*Hindeodella ibergensis*	*Hindeodella mehli*	*Hindeodella uncata*	*Hindeodella undata*	*Hindeodella* sp	*Idiognathoides noduliferus inaequalis*	*Idiognathoides noduliferus japonicus*	*Idiognathoides noduliferus noduliferus*	*Idiognathoides* ? sp	*Kladognathus* sp	*Ligonodina roundyi*	*Ligonodina* sp	*Lonchodina bischoffi*	*Lonchodina ponderosa*	*Lonchodina* sp	*Neoprioniodus scitulus*	*Neoprioniodus singularis*	*Neoprioniodus* sp	*Ozarkodina delicatula*	*Ozarkodina* sp	*Rhachistognathus muricatus*	*Rhachistognathus primus*	*Spathognathodus campbelli*	*Spathognathodus scitulus*	*Spathognathodus* sp	*Streptognathodus lateralis*	*Streptognathodus* ? sp	*Subbryantodus subaequalis*	*Synprioniodina microdenta*	*Synprioniodina* sp	Gen indet	Total	Sample weight in kilograms	Concentration of conodonts in spec/kg
BUKIT TINGGIK	T146															2				6	11						1					1		1	2					1	1					11	37	2.0	18
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	BT19														1					1	3		4											1							2					11	23	2.5	9
	619																			2	4		1												1											3	11	2.0	5
	618							1												11	12		5											1	3						3			1		19	56	2.0	28
	617						1							1		2				14	34	3	6											8	1						2					30	102	3.0	34
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	611														1					8	2																			1						3	15	2.0	8
	610							4		2				1		1		1		24	6									1		1		1										2		13	59	2.0	30
	609						1	1												17	6		3											1	2											7	38	2.0	19
	608																			2															1											1	4	2.0	2
	607																																														0	2.0	0
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	586																			8		6	7	1										2		1										5	30	4.0	7
	585															1				6	14	3	28	5										6	1	1	1				1			1		23	91	3.5	25
	584																																														0	2.0	0
	613																																													3	3	2.0	1.5
	614			1																																											1	2.0	0.5
	583																																														0	2.0	0
	582																			2																					1					6	9	2.0	4
	578				1			3	1		1		1			2				42	4		1				1	1			1	3		4	5			1			1			2		24	99	4.0	25
	577						1	3			2									1							1											1								8	18	3.5	5
	576																																														0	3.0	0
	575					2	14		2			2								29	31			6									2		10			4			4	2		1	2	56	167	7.0	24
	581																			1	3																									4	8	1.0	8
	580						2								1					7	17			1	1				1					1								1				17	50	6.0	8
	579	1	1					1												11	22		9	1										4				1	1		2			1		65	120	9.0	13
BUKIT PANCHING	615																																														0	2.0	0
	594																																													2	2	2.0	1
	593																																								1						1	2.0	0.5
	592																																														0	2.0	0
	591																																													4	4	2.0	2
	590																				1																									3	4	2.0	2
	589																																														0	2.0	0
	588					2		8				1		3		7	3		1	67	9				1	1	1	2			1	5		2	2						4		4			24	148	5.5	27

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Correlation with Europe. The sequence of Namurian conodont faunas in Europe is poorly known except in northern England, where Higgins (1975) has recognized seven zones and four subzones

<table>
<tr><th rowspan="2">Series</th><th rowspan="2">European goniatite Zones</th><th colspan="2">West Malaysia (This paper)</th><th colspan="2">Britain (Higgins 1975)</th><th>Japan (Koike 1967, Igo *et al.* 1978)</th><th>Nevada, Utah (Dunn 1970)</th><th>Arkansas, Oklahoma (Lane and Straka 1974)</th></tr>
<tr><th>Zone</th><th>Subzones</th><th>Zone</th><th>Subzones</th><th>Zones</th><th>Zones</th><th>Zones</th></tr>
<tr><td rowspan="5">NAMURIAN</td><td>? H_{2a}</td><td rowspan="4">*Idiognathoides noduliferus – Streptognathodus lateralis*</td><td rowspan="3">*Idiognathoides noduliferus japonicus – Rhachistognathus*</td><td rowspan="5">*Idiognathoides noduliferus – Streptognathodus lateralis*</td><td rowspan="4">*Idiognathoides noduliferus*</td><td rowspan="3">*Gnathodus bassleri bassleri*</td><td rowspan="3">*Rhachistognathus*</td><td rowspan="2">*Rhachistognathus primus*</td></tr>
<tr><td rowspan="3">H_{1b}</td></tr>
<tr><td>*Rhachistognathus muricatus*</td></tr>
<tr><td>*Idiognathoides noduliferus inaequalis – Gnathodus commutatus*</td><td rowspan="2">*Gnathodus bilineatus – Idiognathoides noduliferus*</td><td rowspan="2">*Gnathodus girtyi simplex*</td><td rowspan="2">*Adetognathus unicornis*</td></tr>
<tr><td>H_{1a}</td><td colspan="2"></td><td>*Idiognathoides minutus*</td></tr>
</table>

TEXT-FIG. 4. Comparisons of early Namurian conodont zonations.

spanning the interval from late Dinantian to early Westphalian, and in Belgium (Higgins and Bouckaert 1968). The faunas of the Panching limestone are similar to those assigned by Higgins to the *I. noduliferus–S. lateralis* Zone, which is equivalent to the E_{2c} to H_{2c} goniatite zones. The upper fauna lacks any of the typical Kinderscoutian forms recorded by Higgins and is characterized by *I. noduliferus japonicus* which first occurs in Higgins and Bouckaert's (1968, p. 21) 'upper' fauna of H_{1b} in Belgium, and in H_{2a} in northern England: it is therefore likely to be of Alportian and possibly late Chokierian age. The lower fauna lacks *I. minutus*, characteristic of the late Arnsbergian and early Chokierian of northern England, and is therefore likely to be of late Chokierian age (H_{1b}).

The lower fauna from the Panching limestone contains *Gnathodus* spp., which was not recorded by Higgins (1975) from levels above E_{2c} in northern England. *Gnathodus* spp., however, do occur in H_{1b} in Belgium (Higgins and Bouckaert 1968, p. 21), and Higgins (pers. comm. 1978) has reported *G. bilineatus bollandensis* from the Alportian (H_2) of north Staffordshire, England.

Correlation with Japan. Watanabe (in Igo *et al.* 1978, fig. 14) recognized four conodont zones for the Omi Limestone in central Japan, from oldest to youngest, the *G. bilineatus* Zone, *S. noduliferus* Zone, *S. expansus–S. suberectus* Zone, and *G. roundyi–I. delicatus* Zone. The middle and upper part of Watanabe's *S. noduliferus* Zone corresponds to the lower part of the *Profusulinella* fusuline zone and is therefore younger than the Panching limestone which contains an *Eostaffella–Millerella* Zone fauna (Ozawa 1975). The conodont faunas of the Panching limestone must therefore correlate with the lower part of Watanabe's *S. noduliferus* Zone which corresponds to the limestone conglomerate horizon of the Omi Limestone.

Koike (1967) proposed seven conodont zones for the late Mississippian to early Pennsylvanian Atetsu Limestone of south-west Japan. These zones are being modified by Koike (pers. comm.). In his revised zonation, Koike will recognize a *G. bilineatus–I. noduliferus* Zone (= *G. bilineatus–G. nodulifera* Zone of Koike 1967) at the top of the Nagoe Formation and an *I. noduliferus* Zone (= lower part of the *G. wapanuckensis* Zone of Koike 1967) at the base of the succeeding Kodani Formation. The *G. bilineatus–I. noduliferus* Zone of the Atetsu Limestone is correlated with the *I. noduliferus inaequalis–G. commutatus* Subzone of the present work since they both have an association of *I. noduliferus*, *G. bilineatus*, and *G. commutatus*. The overlying *I. noduliferus* Zone of Koike (1978 pers. comm.) is equivalent to the lower part of the *G. bassleri bassleri* Zone of Igo *et al.* (1978, tables 2, 3) and is here tentatively correlated with the *I. noduliferus japonicus–R.* Subzone of the present work.

Correlation with North America. Dunn (1970*b*) described the conodont zonation near the Mississippian–Pennsylvanian boundary in Nevada and Utah. He recognized a *R.* Zone which contained the Mississippian–Pennsylvanian boundary and correlated this with the upper part of the Chokierian Stage (H_1) of Europe. Lane and Straka (1974) working in Arkansas and Oklahoma recognized a lower *R. muricatus* Zone and an upper *R. primus* Zone and the boundary between these zones was shown to coincide with the Mississippian–Pennsylvanian boundary. Lane and Straka agreed with Dunn (1970*b*) in placing the boundary in H_1 and suggested it correlated with the upper part of the *Homoceras beyrichianum* goniatite zone (H_{1b}) of Europe. Both *R. muricatus* and *R. primus* are recorded from the upper part of the Panching limestone. This suggests that the *Rhachistognathus* zones of Dunn (1970*b*) and Lane and Straka (1974) correlate with the *I. noduliferus japonicus–R.* Subzone of the present work.

Correlation with European sections (see above) indicates that the H_1/H_2 boundary probably occurs in the uppermost part of the Panching limestone. The Mississippian–Pennsylvanian boundary would therefore fall in H_{1b} which agrees with correlations proposed by Dunn (1970*b*) and Lane and Straka (1974).

CONCLUSIONS

The Panching limestone conodont faunas represent the *I. noduliferus–S. lateralis* conodont zone of Britain and are of H_{1b} and possibly H_{2a} age. Two subzones are recognized in the Panching limestone, a lower *I. noduliferus inaequalis–G. commutatus* Subzone and an upper *I. noduliferus japonicus–R.* Subzone. The Mississippian–Pennsylvanian boundary may be correlated with a level in the upper part of the Panching limestone of Pahang, West Malaysia.

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NON-AUTOSTYLIC PENNSYLVANIAN INIOPTERYGIAN FISHES

by BARBARA J. STAHL

ABSTRACT. Further study of iniopterygian fishes from the Pennsylvanian of North America has shown that autostylic jaw suspension is not, as was originally thought, a characteristic of the group. Two of the five genera possess palatoquadrate elements that articulate with the neurocranium, a fact that calls for modification of the history of the mandibular arch tentatively proposed for these fishes.

No problem has proved more puzzling to students of lower vertebrates than the evolution of the Palaeozoic chondrichthyan fishes. Studies of Recent forms show the association of elasmobranchs and holocephalians in the class Chondrichthyes, but within that category much remains to be clarified, particularly concerning the interrelationships of the oldest forms. Until recently, holocephalians could be traced through the fossil record only to the Jurassic. Association of earlier forms with this group was highly speculative. In the case of the elasmobranchs, Palaeozoic representatives have long been known, but they are variously specialized, and the nature of their relationship is not evident. The origin of all these cartilaginous fishes is rooted in or near the extinct Placodermi. Moy-Thomas and Miles (1971) regarded the chondrichthyans as diverging from placoderms and then differentiating into elasmobranchs and holocephalians. Others suggested the evolution of elasmobranchs and holocephalians from separate placoderm ancestors (Ørvig 1960; Stahl 1967).

During the last twenty-five years a significant number of chondrichthyan fishes has been recorded from sediments of Carboniferous age in the American mid-continent. Proof that broad diversification of this group existed in the shallow marine and brackish waters that covered the area extending from Indiana west to Kansas and Nebraska, and northward into Montana, indicates that in earlier Palaeozoic times a radiation of chondrichthyans—perhaps geographically very broad—had taken place, of which palaeontologists were barely aware. Zangerl (1973) lists six groups of elasmobranchs on the basis of distinctive body design, and Zangerl and Case (1973) describe a new order of chondrichthyan fishes, the Iniopterygia, whose relationships have yet to be defined. If, however, the newly discovered fossils complicate the history of the class Chondrichthyes, they also provide more evidence to elucidate it.

The discovery of the Iniopterygia is regarded as particularly interesting because the fishes in this group share derived characters with the chimaeroid holocephalians, and may thus reveal something about the affinities of the latter group. Although the iniopterygians show structural similarities to both elasmobranchs and chimaeroids, they are surely not phylogenetic intermediates. Their own structural specializations—notably the dorsally placed articulation of the pectoral fin basals on the pectoral girdle—make that idea implausible.

Zangerl and Case reconstructed the iniopterygian fishes as being chimaeroid in body-form: stout anteriorly with the reduced caudal musculature characteristic of leisurely swimmers (text-figs. 1 and 2). They thought that the fishes propelled themselves to some extent with wing-like movements of the broad pectoral fins. The skull of the iniopterygians was relatively short, with the gill arches crowded forward under an operculum stiffened by cartilaginous rays attached to the hyoid elements. Like elasmobranchs, their teeth were separate (at least at the cusps) and organized in tooth families. They had, as did the Palaeozoic sharks, long radial cartilages in the pectoral and caudal fins, and a long-jawed terminal mouth.

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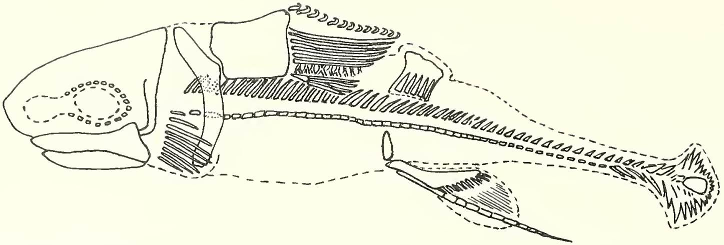


TEXT-FIG. 1. *Iniopteryx rushlaui.* Reconstruction of skeleton and outline of body. Modified from Zangerl and Case.

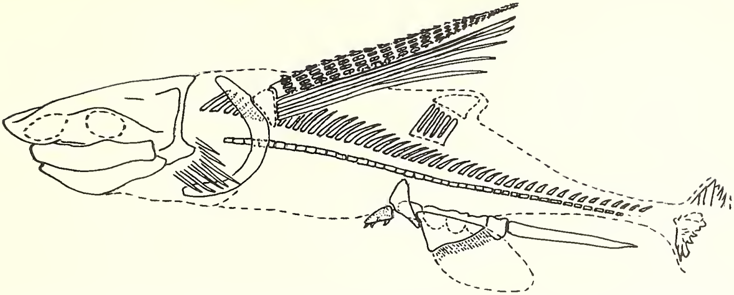
Zangerl and Case stated initially that the palatoquadrate cartilages were fused to the neurocranium in iniopterygians as they are in chimaeroid holocephalians. Classifying these two kinds of fishes in sister-groups—the orders Iniopterygia and Chimaerida of the subclass Holocephali of the class Chondrichthyes—the senior author supposed autostyly to be a shared, derived (synapomorphous) character that distinguished holocephalian from elasmobranch chondrichthyans.

The discovery that autostyly is not characteristic of all the iniopterygians has implications not only for the history of these fishes but also for the origin of the chimaeroids.

MATERIAL AND METHODS

The iniopterygians whose jaw suspension is described here as being non-autostylic are *Iniopteryx rushlaui* and *Promexyele peyeri,* forms placed in the family Iniopterygidae. They are known from the Wea Shale and the Stark Shale, upper Westphalian D (*Iniopteryx*) and the Labette Black, Excello, Mecca Quarry, and Logan Quarry Shales, lower Westphalian D and C (*Promexyele*) of the Pennsylvanian. The new specimens discussed in this paper were obtained from the Mecca Quarry Shale at Hesler quarry, Parke County, Indiana, and were collected by a Field Museum of Natural History (FMNH) party in 1973. At this site both *Iniopteryx* and *Promexyele* are relatively common. Only those specimens with the most favourable preservation of the braincase and/or branchial elements were studied: *I. rushlaui*: PF 3098, PF 8560, PF 8561, PF 8562, PF 6661, PF6677; *P. peyeri*: PF 8563, PF 8564, PF 8565, PF 8026, PF 8566, PF 2358, all in the collection of the Field Museum of Natural History, Chicago.

Since the specimens, composed of calcified cartilage, are wholly covered by the shale in which they are embedded and cannot be exposed by removing the matrix, they were studied in stereoscopic X-rays prepared by the method described by Zangerl (1966). The use of the stereoscopic technique makes it possible to reconstruct the three-dimensional form of the braincase and to differentiate branchial elements that are superimposed in the shale. Interpretation of the fossils is complicated by the fragmented or twisted state of some of the branchial elements and by a reduction in the depth of those braincases preserved with their dorsal and ventral surfaces parallel to the bedding plane of the shale. Deformation of the braincases is not extreme, because it resulted from the slight settling of the mineralized material of the skeleton, in loose, undisturbed sediment, as the organic cartilaginous framework holding the crystals gradually decayed. Subsequently little or no compression took place. Since a braincase of *Iniopteryx* preserved in lateral orientation was available (text-fig. 3), the vertical dimension of the skull in that form could be reconstructed with a relatively high degree of confidence. The accuracy of the form of the branchial elements used in the reconstructions was checked, where possible, by comparing homologous elements in two or more specimens.

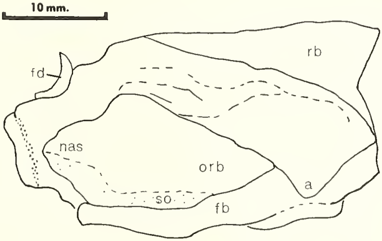


TEXT-FIG. 2. *Promexyele peyeri.* Reconstruction of skeleton and outline of body. Modified from Zangerl and Case.

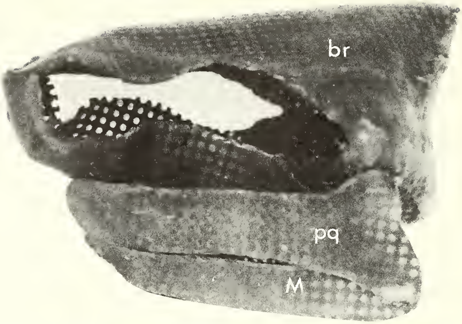
To verify the anatomical relationships visualized from the X-rays, three-dimensional models of *Iniopteryx* and *Promexyele* were made (text-figs. 4 and 5). Association in the shale of the braincase and branchial elements supports this reconstruction which produces a head skeleton that could have fulfilled the functions it served in life.

OBSERVATIONS

In both *Iniopteryx* and *Promexyele* the braincase lacks the pair of densely mineralized facettes that is present on the ventral surface beneath the posterior margin of the orbits in *Iniopera* and *Sibyrhynchus* (the braincase of *Inioxyele* is not known well enough to make description of this area possible). These facettes, which faced anteriorly from robust ventrolateral protrusions of the braincase in the latter two genera, were identified by Zangerl and Case as points of articulation of the lower jaw. In the absence of these abutments for Meckel's cartilages, the neurocrania of *Iniopteryx* and *Promexyele* appear more similar to the braincases of contemporary sharks than to those of chimaeroid



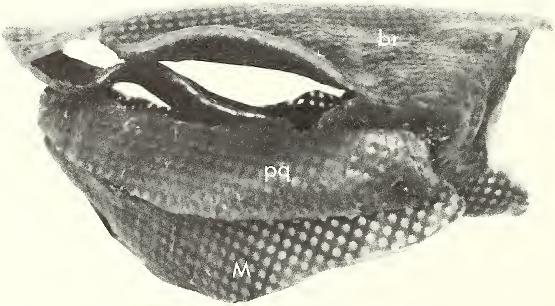
TEXT-FIG. 3. *Iniopteryx rushlaui.* FMNH PF 8560. Lateral view of braincase. Drawn from radiograph. a, area of articulation for palatoquadrate; fb, floor of braincase; fd, displaced fin ray denticle; nas, nasal cavity; orb, orbit; rb, roof of braincase; so, suborbital shelf.



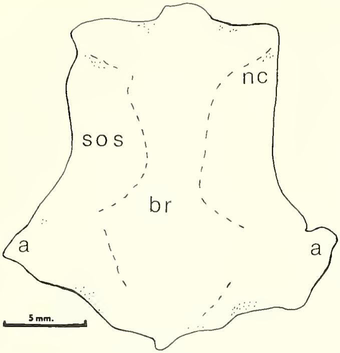
TEXT-FIG. 4. *Iniopteryx rushlaui*. Model of braincase and mandibular arch in lateral view. br, braincase; M, Meckel's cartilage; pq, palatoquadrate.

holocephalians. In both genera, the posterior part of the braincase is short: in *Iniopteryx* (text-fig. 6) the region posterior to the orbit is about a third, and in *Promexyele* (text-fig. 7) slightly more than a third, of the length of the skull. In each, the supraorbital shelf continues posteriorly into a postorbital process that curves ventrad and bears at its terminus a surface that is shaped as if it were a point of articulation. This projection is supported from below by a densely mineralized strut that extends dorsolaterally from the floor of the braincase behind the orbit.

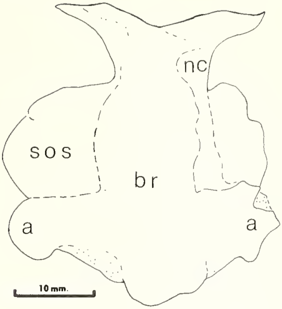
Although the end of the postorbital process is not reinforced by as dense a layer of mineral crystals as exists on the facettes for the lower jaw in *Iniopera* and *Sibyrhynchus*, it still seems likely that it was the point of attachment for a jaw element. The surface bears a shallow groove in which an opposing cartilage could have ridden fore and aft, and the postorbital process, with its ventrally supporting



TEXT-FIG. 5. *Promexyele peyeri*. Model of braincase and mandibular arch in lateral view. br, braincase; M, Meckel's cartilage; pq, palatoquadrate.



TEXT-FIG. 6. *Iniopteryx rushlaui.* FMNH PF 3098. Braincase in dorsal view. Drawn from enlarged radiograph. a, area of articulation for palatoquadrate; br, braincase; nc, nasal capsule; sos, supraorbital shelf.



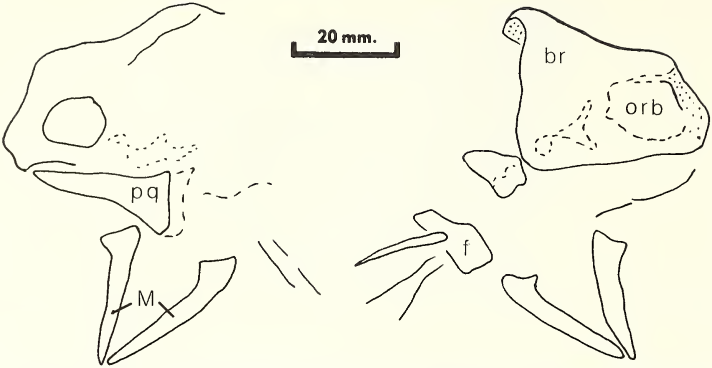
TEXT-FIG. 7. *Promexyele peyeri.* FMNH PF 8563. Braincase in dorsal view. Drawn from enlarged stereoradiographs. a, area of articulation for palatoquadrate; br, braincase; nc, nasal capsule; sos, supraorbital shelf.

strut, forms a mechanical arch through which stress would have been projected dorsally and ventrally against the more central part of the braincase.

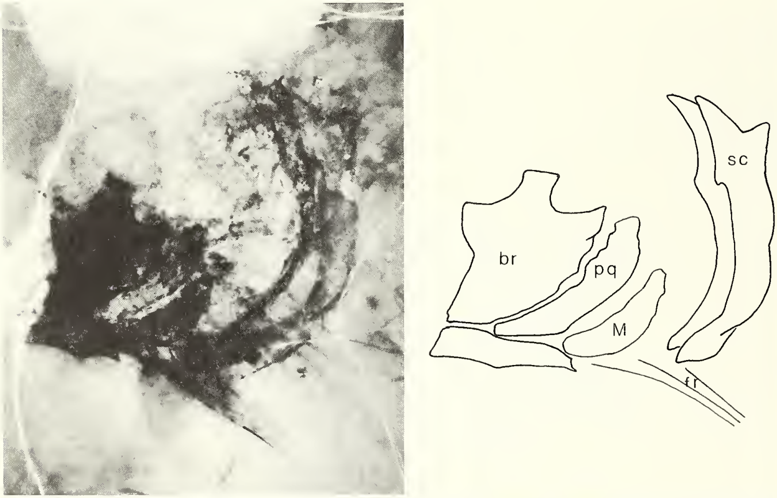
In both *Iniopteryx* and *Promexyele*, the ventral surface of the braincase narrows anterior to the struts that extend to support the postorbital articular processes. The resulting space left ventral to the orbit and posterior to the laterally flaring nasal capsule accommodates the greater part of the palatoquadrate when that element is placed in articulation with the end of the postorbital projection. No anterior articulating process is clearly evident on any of the palatoquadrate cartilages through which a second abutment against the braincase could have been made, but the tip of the palatoquadrate fits snugly against the neurocranium ventral to the nasal capsule, allowing the possibility of a ligamentous tie in that area for greater stability.

The form of the palatoquadrate and mandibular elements in both *Iniopteryx* and *Promexyele* is similar to the basic structure of epibranchial and ceratobranchial arch elements. Whether their lack of greater specialization is primitive or secondary cannot be decided on the evidence available. The palatoquadrate, rather than possessing the broadly expanded posterior end with the otic process characteristic of sharks, is much more uniform in width along its length. In *Iniopteryx*, the palatoquadrate can be identified in only two specimens, PF6677 (text-fig. 8) and PF6661. In both, the element is only slightly flared posteriorly, where it articulates with the braincase dorsally and the mandible ventrally. The body of the palatoquadrate is a little broader than that of the lower jaw and tapers at the anterior end. The palatoquadrate of *Promexyele* is even more bar-like (text-fig. 9A), neither widening posteriorly nor tapering at the front. The element has been observed in all the specimens of *Promexyele* examined by the author and has been identified in at least nine others by Zangerl (pers. comm.).

In contrast to the palatoquadrate of *Iniopteryx*, the mandibular elements are clearly seen in numerous specimens. They bear a short, pyramidal process which projects dorsad immediately anterior to the articular facette at the posterior end. The body of the element is straight and narrows to a point anteriorly. Although still relatively simple in design, the mandibles of *Promexyele* are quite different from those of *Iniopteryx*. In *Promexyele* the lower jaw is bar-like at the rear, but anteriorly



TEXT-FIG. 8. *Iniopteryx rushlaui.* FMNH PF 6677. Braincase with palatoquadrate in place and Meckel's cartilages preserved below. Drawn from the fossil directly. Plate at left; counterplate at right. Note superimposition of palatoquadrate cartilages visible on plate. br, braincase; f, fin elements; M, Meckel's cartilage; orb, orbit; pq, palatoquadrate.

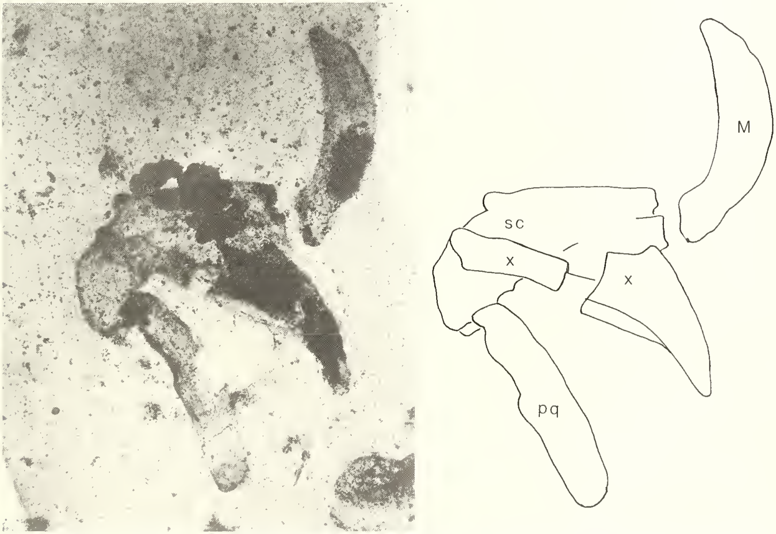


TEXT-FIG. 9A. *Promexyele peyeri.* FMNH PF 2358. Skull and pectoral girdle in lateral view with jaw elements approximately in place. Radiograph ×1. Explanatory sketch alongside. br, braincase; fr, fin rays; M, Meckel's cartilage; pq, palatoquadrate; sc, scapulocoracoid.

one edge is straight and the other broadly curved (text-fig. 9B). Frequently, a row of tooth-wells can be seen parallel to the long axis of the element in its broadest portion.

In life, neither the palatoquadrate nor Meckel's cartilage was fused to its counterpart on the opposite side. Since the elements of the mandibular arch in *Iniopteryx* and *Promexyele* have never been found united with their opposite members (unlike the Meckel's cartilages in *Iniopera* and *Sibyrhynchus*), the upper and lower jaw cartilages are assumed to have been bound by ligaments to those of the other side, or perhaps, in the case of the lower jaw, to have abutted a small median cartilage which has gone unrecognized in the specimens studied.

The branchial skeleton posterior to the first arch is composed of more delicate elements that are fragmented in the available specimens, and generally preserved inextricably jumbled in a narrow plane. It is therefore not possible to describe with certainty the structure of the hyoid arch or its exact spatial relationship to the jaws. The presence of what appears to be a small, curved flange on the rear of the braincase posterodorsal to the articular surface for the palatoquadrate may well have been the point of attachment for the epihyal cartilage. The flange is suggested, rather than clearly preserved on some of the braincases, so only the most tentative suppositions should be based upon it. Observations suggest that the articular surface rimmed by the small flange faced posteriorly. If this were the case, the epihyal would probably have extended posteriorly, and therefore may not have come in contact with the jaw-joint to support it.



TEXT-FIG. 9B. *Promexyele peyeri*. FMNH PF 8563. Jaw elements disarticulated and displaced. Radiograph × 2. Explanatory sketch alongside. M, Meckel's cartilage; pq, palatoquadrate; sc, scapulocoracoid; x, unidentified elements.

DISCUSSION

The existence of iniopterygian fishes with autostylic and non-autostylic jaw suspension raises numerous questions concerning the adaptation and phylogenetic history of the group. Palaeontologists generally seek to distinguish the geographical range and the particular habitat of the animals in question and then to link the acquisition of specialized structures to the niches and natural selective forces that they have defined. As a general rule, they discover some correlation between the animals' feeding habits and mode of locomotion expressed in co-ordinated structural modifications. The iniopterygian fishes present a paradox: although jaw suspension within the group differs in a way that is functionally significant, they were essentially sympatric and appear to have shared the same environment. The deposition of their remains in similar shales in the shallows edging the Pennsylvanian epicontinental sea demonstrates their common exposure to a peculiar and restrictive set of conditions described by Zangerl and Richardson (1963). They believe that in these waters, there was no bottom-dwelling fauna because of toxic compounds from anaerobic decomposition that occurred in the dense, quiet mud. Therefore, unable to live like holocephalians on hard-shelled molluscs and other bottom-living invertebrates the autostylic iniopterygians, like their non-autostylic relatives, would have been confined to the mass of water-weed that floated above the mud. Doubtless, the smaller animals in the weeds together with the plant material would have sustained the slow-swimming iniopterygians. The palaeohabitat in which the iniopterygians have been discovered offers no evidence to elucidate the circumstances which favoured, in the same order, the retention of an identical body-form (and hence the same locomotor style) and the development of both autostylic and non-autostylic jaw suspension, arrangements that imply different diets. Further insight awaits the finding of these forms in other locations where environmental conditions were less transient and offered a greater variety of niches.

The presence of non-autostylic iniopterygians poses a problem for modern taxonomists whose classification schemes are intended to reflect evolutionary relationships. In their view, the autostyly of the extant chimaerids is one of the chief traits that separates these fishes from elasmobranchs. In regarding jaw suspension as a key character, current workers are following a practice that has influenced the interpretation of piscine relationships for many years. Huxley (1876) used autostyly to distinguish lungfishes from bony fishes in which the hyomandibular gave support to the jaws. Gregory (1904), arguing that the autostyly of chimaerids was different from that which appeared in lungfishes, called the chimaerid form of jaw suspension holostyly. The fusion of the palatoquadrate with the braincase led to the name Holocephali for the taxon housing the chimaerids, and Patterson's (1965) attempt to classify a wide variety of bradyodont chondrichthyans as holocephalians was resisted by Zangerl and Case and by Lund (1977*a*), because there were non-autostylic forms among those fishes. Zangerl included the Iniopterygia within the Holocephali because, in addition to the opercular flap and general body-form, the members of the group seemed to have had the upper jaw fused to the neurocranium. His description of the Iniopterygia and the Chimaerida as sister-groups implied the evolution of holostyly in a common ancestor, presumably a divergent elasmobranch that formed the root of the holocephalian line. The description by Lund (1977*b*) of a chimaeriform fish from the late Mississippian Bear Gulch limestone of Montana favoured Zangerl's evolutionary hypothesis.

Unless the non-autostyly of *Iniopteryx* and *Promexyele* is secondary, which seems unlikely, it must now be assumed that the common ancestor of the iniopterygians and the chimaerids had a palatoquadrate suspended in shark-like fashion. The first holocephalians would not have merited the name, and autostyly or holostyly would have evolved in fishes of this group at least twice. Positing the independent and parallel evolution of an autostylic palatoquadrate within the Holocephali is not of great help in determining the origin of the group, but it does tie the holocephalians more closely to the elasmobranchs and makes alliance with any other forms remote. One may speculate, as the classification scheme of Arambourg and Bertin (1958) implies, that the holocephalian fishes expressed in the most extreme form the tendency among a number of early Palaeozoic chondrichthyans to develop fusions of teeth, jaws, and neurocranium. In other lines that took this evolutionary course, grouped by Arambourg and Bertin as Eubradyodonti, tooth whorls or tooth plates appeared, but autostyly was rarely if ever reached.

If the non-autostylic iniopterygians were archaic in retaining a jaw suspension resembling that of their ancestors, it is reasonable to look to them for clues to the primitive condition of the mandibular and hyoid arches. Besides the discrete and unspecialized form of the jaw elements, the most striking characteristic of the first arch is the relative fragility of the palatoquadrate. In *Iniopteryx*, which had rows of very small conical teeth, suggestive of a weak bite, the upper jaw cartilage, unlike the mandibular element, is not generally preserved without breakage or deformation. In neither *Iniopteryx* nor *Promexyele* does the palatoquadrate present broad or tall projections that would have afforded an area of attachment for strong ligaments tying the upper jaw to the neurocranium. The palatoquadrate in these iniopterygians is thus unlike the homologous element in the Pennsylvanian sharks *Cobelodus*, *Denaea*, and *Symmorium*, that Zangerl and Williams (1975) regard as primitive. In these elasmobranchs, the palatoquadrate, possibly not supported by the epihyal element of the second arch, is expanded posteriorly and braced firmly against the braincase through three abutments. In the opinion of Zangerl and Williams this rigid attachment of the palatoquadrate gave way to arrangements that provided greater freedom of movement in more advanced elasmobranchs. If that hypothesis is correct, and the design, primitive for sharks, is also primitive for gnathostomes, the structure and style of attachment of the upper jaw in the non-autostylic iniopterygians would have to be considered secondary rather than reflective of an early stage in the transformation of a branchial arch into jaws.

Evidence concerning the structure of the hyoid arch is insufficient to support speculations about its suspensory function. Logic suggests, and Watson (1937) and Zangerl and Williams state, that the earliest gnathostomes probably had an unspecialized hyoid arch separated far enough from the mandibular arch to allow a full gill slit between them; a condition described by Watson as aphetohyoidean. If the Pennsylvanian elasmobranchs analysed by Zangerl and Williams were in fact aphetohyoidean, and if the condition were to be found in the Iniopterygia, the possibility that aphetohyoidy was present in the earliest gnathostomes would be enhanced. Available fossil material provides for *Iniopteryx* and *Promexyele*, no regularly identifiable complete hyoid arch elements that would give certainty to a reconstruction. The orientation of the facette on the braincase that apparently provides an abutment for the epihyal suggests, besides the absence of a pharyngohyal, that the epihyal was directed posteriorly; an arrangement that would have left a space between the first and second arches. However, the possibility that that space would have contained a gill slit seems diminished by the operculate character of the iniopterygian fishes. In extant operculate forms (both in the chimaerids and bony fishes), the gill arches are crowded and set forward under the rear of the braincase. As a result, the prehyal slit is never present except as a spiracle, and is usually obliterated altogether. Since the delicacy of the branchial arch elements apparent in the iniopterygians suggests a similar reduction and crowding in the gill region, it seems more probable to speculate against aphetohyoidy in these fishes.

CONCLUSION

The discovery that the palatoquadrate cartilage is not fused to the neurocranium in *Iniopteryx* and *Promexyele* requires the removal of autostyly as a characteristic of the family to which these genera belong. The taxonomist is thus left with fishes within the sub-class Holocephali that are surely quite closely related to other holocephalians and yet lack a diagnostic feature of the group. Implications relating to the phylogeny of the holocephalians are also apparent: the source of the line was most likely not a population of sharks that had evolved fusion of the upper jaw and braincase, but one that possessed the genetic potential for doing so. Presumably, as the stock diversified, autostyly evolved in parallel. In their jaw suspension, *Iniopteryx* and *Promexyele* would have been archaic forms.

Whether these iniopterygians retained traces of the arrangement of the first two branchial arches that was primitive for chondrichthyans or gnathostomes generally, is less clear. Resolving this question, as well as understanding the selective forces that produced functionally very different jaws in iniopterygians of similar body-form, will be possible only if earlier Carboniferous and Devonian cartilaginous fishes are found.

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THE EUROPEAN SPECIES OF THE CRETACEOUS AMMONITE *ROMANICERAS* WITH A REVISION OF THE GENUS

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ABSTRACT. The genus *Romaniceras* Spath, 1923, is shown to be a member of the subfamily Euomphaloceratinae Cooper, 1978, derived probably from *Kamerunoceras* Reyment, 1954. Three subgenera are recognized: *R.* (*Romaniceras*), *R.* (*Yubariceras*) Matsumoto, Saito, and Fukada, 1957, and *R.* (*Obiraceras*) Matsumoto, 1975. The European Turonian yields three successive species: *R.* (*R.*) *kallesi* (Zázvorka), of which *R. hispanicum* Wiedmann is a synonym; *R.* (*Y.*) *ornatissimum* (Stoliczka), of which *R.* (*Y.*) *deverioides* (de Grossouvre) and *R.* (*Y.*) *yubarense* Matsumoto, Saito, and Fukada are the most important synonyms; and *R.* (*R.*) *deverianum* (d'Orbigny) of which *R.* (*R.*) *uchauxiense* Collignon, *R.* (*R.*) *medlicottianum* (Stoliczka), *R.* (*R.*) *pseudodeverianum* (Jimbo), and *R.* (*R.*) *yezoense* Matsumoto are the most important synonyms.

Dimorphism is tentatively recognized in *R.* (*Y.*) *ornatissimum*, and it is shown that there is a high degree of intraspecific and ontogenetic variability in both *R.* (*Y.*) *ornatissimum* and *R.* (*R.*) *deverianum*, comparable to that seen in other acanthocerataceans.

ROMANICERAS Spath, 1923, is a widespread and frequently quoted genus of multituberculate acanthoceratids of world-wide distribution and of great importance in the correlation of mid and late Turonian successions. This is especially true in Touraine, the type area of the Turonian stage (see discussion in Hancock, Kennedy, and Wright 1977) whilst the genus also provides a link between the collignoniceratid-dominated faunas of Europe and north America and those of more southerly areas dominated by pseudotissotiids and vascoceratids. A considerable number of species has been erected and referred to the genus, although re-examination of the type material of the older European species, such as *Romaniceras deverianum*, shows that many of these are unnecessary. Moreover, various other genera and subgenera have been created for Turonian multituberculate forms and the assignation of species to these varies widely. A revision of the rich European faunas, especially those of Touraine and Uchaux (Vaucluse), is thus long overdue in order to clarify the relationships of the numerous Japanese, American, and other species, as well as to provide a firmer basis for the subdivisions and correlation of the Turonian stage.

SYSTEMATIC PALAEONTOLOGY

Dimensions. Dimensions of specimens are given in millimetres, in the following order: diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U). C and IC refer to costal and intercostal dimensions. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullmann and Wiedmann 1970) is followed in the present work, where I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Techniques. Specimens were photographed on Kodak Pan F 35 mm film, ASA rating 50, using a Pentax reflex camera with a 1:2/55 super Takumar lens. In many cases whitening before photography was found to be unnecessary, especially with Tuffeau specimens.

Suture lines were drawn using a Wild Binocular Microscope with *camera lucida* attachment.

Abbreviations used for collections. AM, Musée de Paléontologie d'Angers; BMNH, British Museum (Natural History), London; EMP, Ecole des Mines, Paris (now housed at the Université Claude Bernard, Lyon); FSL, Faculté des Sciences, Université Claude Bernard, Lyon; FSM, Faculté des Sciences, Le Mans; chiefly collections formerly housed in the Musée de Tessé, Le Mans; FSR, Institut de Géologie, Université de Rennes; GK, Department of Geology, Kyushu University, Fukuoka; GT, University of Tokyo Museum; LC, Lecointre collection in

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the Chateau du Grand-Pressigny, Indre-et-Loire; MN, Muséum d'Histoire Naturelle, Nantes; MNHP, Muséum National d'Histoire Naturelle, Paris; OUM, University Museum, Oxford; unless stated otherwise, these are collections made by Hancock and Kennedy; SP, Collections of the Sorbonne, now Université de Paris VI; WW, C. W. and E. V. Wright collection.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family ACANTHOCERATIDAE de Grossouvre, 1894
Subfamily EUOMPHALOCERATINAE Cooper, 1978
Genus ROMANICERAS Spath, 1923

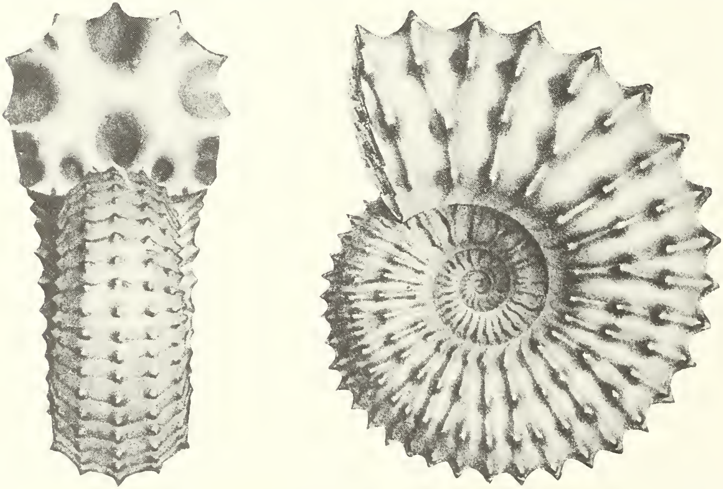
Type species. Ammonites deverianus d'Orbigny, 1841 by the original designation of Spath 1923.

Diagnosis. Rather variable acanthoceratids that are evolute and medium sized to large. Whorl sections are moderately compressed to moderately depressed, quadrate or rounded. Early whorls are smooth and bear periodic constrictions with associated ribs. Middle growth stages have long ribs bearing nine, eleven, or thirteen rows of tubercles of unequal strength and spacing. The nine rows are umbilical, lateral, inner and outer ventrolateral, and siphonal; in species with eleven rows the inner ventrolateral may be doubled and in those with thirteen rows, both inner and outer ventrolateral may be doubled at some stage in ontogeny. Short ribs are intercalated on the flank and bear a full ventrolateral complement of tubercles, with or without laterals. Ribs may also bifurcate from the lateral tubercle.

At maturity some or all tubercles are lost; ribs become mainly long and strong and pass uninterrupted across the venter.

The suture line is relatively simple and of basic *Acanthoceras* type, with broad bifid saddles and narrow lobes; all elements have only minor incisions.

Discussion. Spath did not give a diagnosis of this genus. The stability of the genus and the differentiation of its constituent species depend essentially on the interpretation of the type species *Ammonites deverianus* d'Orbigny (1841, p. 356, pl. 110, figs. 1–2) (reproduced here as text-fig. 1):



TEXT-FIG. 1. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). Copy of d'Orbigny's original protograph (1841, pl. 110, figs. 1–2), based on specimens from Uchaux, Vaucluse.

'whilst for *A. deverianus* d'Orbigny . . . generally erroneously included in *Acanthoceras*, the new genus *Romaniceras* is proposed' (Spath 1923, p. 144). The original description and figures, though the latter are as usual no doubt synthetographs, are perfectly clear, and the species is said to be characterized by its inflation and by nine rows of tubercles, while the only locality mentioned is Uchaux (Vaucluse), with specimens in the collections of Requien, Renaux, Matheron, and d'Orbigny. The original type series therefore can only include Uchaux specimens with nine rows of tubercles in these four collections. Despite this obvious fact, attempts have been made to fix types on different bases.

Basse (1937, pp. 180–181) reported that the Renaux collection, which included a specimen stated by d'Orbigny (1841, p. 357) to be jointly with his the basis of his plate 110, figs. 1, 2, had disappeared. Therefore she endeavoured to clarify the situation by considering what specimens survived in the d'Orbigny collection. She said that the one Uchaux specimen preserved in d'Orbigny's collection (in the Muséum d'Histoire Naturelle, Paris), no. 6781, labelled 'T' for type, was a very badly preserved internal mould from which it was impossible to draw up any list of characters. She also found two other specimens, 6781a from Poncé, Sarthe, and 6781*b*, from Montrichard, Loir-et-Cher, which she called co-types. Since they are not from Uchaux, they cannot be 'co-types'; nor are a further two specimens from Poncé numbered 6781a and one from Tourtenay labelled 6781*c* in the d'Orbigny collection. These specimens were probably added to d'Orbigny's collection after 1841 and before it was catalogued in 1858–1860.

Faced with the absence of any good Uchaux specimen, Basse said that she proposed to take the 'co-types' in future as types, and she refigured them (Basse 1937, pl. 8, figs. 1*a*–*b*, 2*a*–*b*; see Pl. 48, figs. 3–4). Subsequently, Collignon (1939, p. 36) recognized that Basse's so-called co-types were not specimens of *Romaniceras deverianum*, having eleven rather than nine rows of tubercles, and belonged to *R. deverioides* (de Grossouvre). He, therefore, designated as lectotype the original of his pl. 9, fig. 1, 1*a*; pl. 8, fig. 2. This specimen from Masiaposa, Madagascar, is clearly also not available for lectotype designation.

The surviving Uchaux specimen in the d'Orbigny collection is illustrated here as Pl. 41, figs. 3–4. It is in the typical Uchaux preservation of red-brown silicified rock, and has the appearance of having lain exposed for many years, since it has been converted to a cinder-like porous cast. Only half a whorl is preserved, with the following dimensions: D (estimated) = 49 mm (100); Wb = 29 mm (0·59); Wh = 22 mm (0·45); U = 16 mm (0·33); Wb: Wh = 1·31.

There are fifteen sharp bullae on the umbilical shoulder, each giving rise to a single rib, but it is not possible to determine directly the number present over the venter. Each rib arises at the umbilical seam and passes backward across the umbilical wall to develop into a sharp bulla which projects into the umbilicus. The flanks of the specimen are badly corroded; no single rib is preserved for the whole width. They are, however, initially radial and then flex gently backwards. No lateral tubercles are preserved and only one inner ventrolateral. Three, possibly four ribs are preserved in the outer ventrolateral region, and, if interpreted as tubercles, they are bullate rather than clavate. Five, possibly six, siphonal tubercles are preserved and these appear to have been rounded. There are thus at the most seven rows of tubercles preserved on the specimen. Since this specimen is from Uchaux, it is obviously a *Romaniceras*, while the whorl section, and in particular the umbilical bullae, are quite distinctive. It is, however, so poor that it can scarcely have served as the basis for d'Orbigny's figure. It is available for lectotype designation, but it would in our view be injudicious to designate so poor a specimen.

Of the remaining collections that include syntypes, the Matheron collection, preserved in the collections of the Muséum d'Histoire Naturelle, Marseille, suffered greatly in the last war; and we were unable to find specimens of Uchaux *Romaniceras* during a visit made in 1971. The Requien collection is preserved in the Musée d'Avignon, but Roman and Mazeran (1913) make no mention of any surviving *Romaniceras*. The collections of Prosper Renaux, thought by Basse in 1937 to be lost, in fact survive in the collections of the Faculté des Sciences, Montpellier. Dr. J. Sornay informs us that some years ago he saw two poor *Romaniceras* in the Renaux collection; one of them was larger than that indicated by d'Orbigny and a slimmer form than that illustrated (= '*R. uchauxiense*' Collignon); the other showed sutures, which d'Orbigny specifically mentions as being unknown ('tous les

échantillons étant pourvus de leur test, il m'a été impossible de les distinguer. J'ai pu seulement apercevoir, par le dessus de la bouche, qu'il y a extérieurement deux lobes de chaque côté du lobe dorsal, et intérieurement un lobe latéral, de chaque côté du lobe ventral'). These specimens have since disappeared but may turn up again.

In all these circumstances it is undesirable to designate a lectotype immediately. The species meanwhile can be perfectly well interpreted from d'Orbigny's description and figures.

From this position a preliminary review of the Turonian multituberculate forms shows that the majority are readily divisible into two groups, one with nine rows of tubercles and the other with eleven. Most of the former are currently placed in *Romaniceras* sensu stricto, but a few in *Yubariceras* Matsumoto, Saito and Fukada, 1957 (type species *Y. yubarense* Matsumoto, Saito, and Fukada, 1957, p. 27, pl. 8, fig. 1*a–b*; pl. 10, fig. 1*a–b*; pl. 11, fig. 1*a–b*; pl. 13, fig. 1*a–b*; pl. 15, fig. 1; text-figs. 8, 9. See Pl. 40, figs. 3–5). Of the species with eleven rows, most have been assigned to *Yubariceras*. Matsumoto *et al.* regarded *Yubariceras* and *Romaniceras* as superficially homoeomorphous offshoots, *Yubariceras* derived from *Calycoceras* of the *newboldi* (Kossmat) group (= *Newboldiceras* Thomel, 1972) (Mantelliceratinae) and *Romaniceras* from *Acanthoceras* (Acanthoceratinae) respectively. They separated the two genera on the basis of *Yubariceras* having quadrate whorls, a rather flat, broad venter, subparallel and less inflated flanks, and tubercles predominant over the ribs, which weaken with growth. Subsequently Matsumoto (1975, pp. 131 et seq.) added to the diagnosis the presence of intercalated ventral ribs and constrictions on juvenile whorls. From an examination of the described *Yubariceras* species we find that these characters do not occur together sufficiently consistently to allow us to maintain them as the basis of a separate genus. *R. deverianum* has constricted inner whorls; there is great intraspecific variation in the relative dominance of ribs and tubercles and rectangular whorled individuals were described both by Sharpe (1857, p. 46, pl. 19, fig. 5*a–b*) and Roman and Mazeran (1913, pl. 3, fig. 2, 2*a*). The only consistent difference that we can apply is the presence of nine rows of tubercles in one group of species and eleven in another. We cannot support the phylogenetic argument for the independent origin of the two groups. The latest *Calycoceras* (*Newboldiceras*) and *Acanthoceras* of the *rhotomagense* (Brongniart) group considered ancestral date from early in the Late Cenomanian, and there is a considerable gap in the record before the first *Romaniceras* from the middle Turonian (Cooper 1978). On the other hand, constrictions on the inner whorls and multituberculation are seen to occur in the *Euomphaloceras–Kamerunoceras* lineage which extends from the Middle Cenomanian to early in the mid Turonian. We have, for instance, a constricted *Kamerunoceras* from the Upper Cenomanian of Shapwick Grange, Devon, near Lyme Regis, which, together with the '*Kanabiceras*' of Freund and Raab (1969, p. 9, pl. 1, figs. 3–6; text-fig. 4*d–f*) from the 'early Turonian' of Israel, support this link. The earliest whorls of *K. eschii* (Solger) (1904, pl. 4, fig. 2*a–b*) are smooth and constricted as in *Romaniceras*, whilst the earliest *Romaniceras*, *R. kallesi* Zázvorka, described below, is slowly expanding and evolute—the over-all shell form, in other words, of a *Kamerunoceras* combined with the decoration of a *Romaniceras*. That there are rare individuals (to be described below) which link the nine- and eleven-row species further confirms them as a monophyletic group within the Euomphaloceratinae, as Cooper (1978) has hinted.

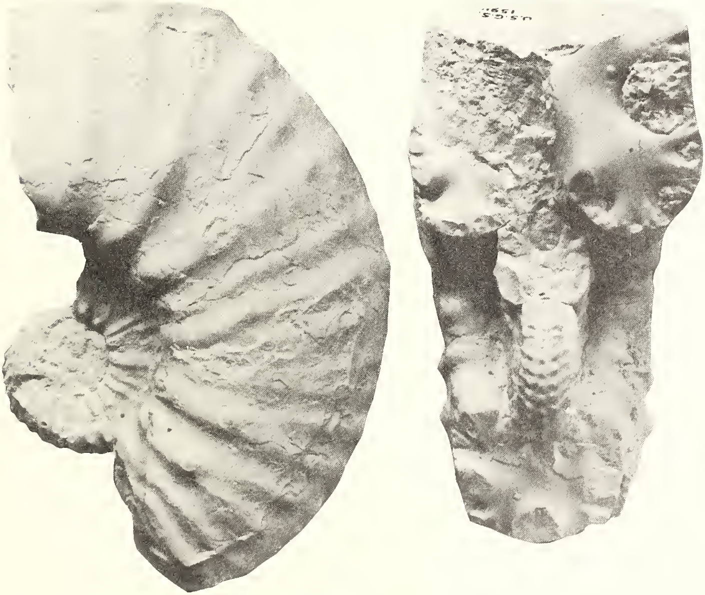
For the record we would note that the Upper Cenomanian *Romaniceras* from the Isle of Wight recorded by Wright and Wright (1951) and cited by Matsumoto as providing an apparent link between the Turonian species and their possible Cenomanian antecedents must be discounted. This specimen (C. W. and E. V. Wright collection no. 10206, loose, ex Middle Cenomanian Lower Chalk, Compton Bay, Isle of Wight, Hampshire) has the inner whorls of a typical *C.* (*N.*) of the *newboldi* group but the umbilical bullae are displaced outwards to an inner lateral position as size increases, as in *C.* (*N.*) *newboldi spinosum* (Kossmat) or *C.* (*N.*) *orientale* Matsumoto, Saito, and Fukada. On the outer, but still septate, whorl, a new bulla develops at the umbilical shoulder, and blunt tubercles develop on the ventrolateral shoulder of one flank to give a *Romaniceras*-like appearance to one side of the specimen. This is presumed to be a minor growth disturbance only.

Obiraceras Matsumoto, 1975 (type species *O. ornatum* Matsumoto, 1975, p. 150, pl. 23, fig. 1; text-fig. 18) was characterized by the doubling of both inner and outer ventrolateral nodes in middle growth (Pl. 40, figs. 1, 6), but is otherwise identical to *Yubariceras*.

These three taxa do not merit separation as genera, given the scale of generic division recognised within the Acanthoceratidae (Wright in Arkell 1957). The differences between the three which can be most consistently applied are the numbers of rows of tubercles and it could be argued that these might be no more than specific criteria. However, the same criteria have been consistently and successfully applied to both Acanthoceratinae (e.g. *Calycoceras*) and Texanitinae (e.g. *Texanites*, *Paratexanites*). The recognition of subgenera *R.* (*Romaniceras*), *R.* (*Yubariceras*) and *R.* (*Obiraceras*) is proposed both as a natural grouping of species and as based on what have proved to be taxonomically useful criteria elsewhere in the Acanthoceratidae.

Comparisons with other genera. Romaniceras are easily distinguished from superficially similar Cenomanian genera such as *Acanthoceras* and *Calycoceras* by the presence of additional rows of tubercles in middle and later growth and by smooth, constricted early whorls.

Shuparoceras Matsumoto, 1975 (type species *S. yagii* Matsumoto, 1975, p. 110, pl. 12, fig. 1, text-fig. 3) is a Turonian genus apparently very close to *Romaniceras*; it should perhaps be treated as a further subgenus. It has a compressed, involute shell with high whorls and ornament of long ribs with nine rows of tubercles during middle growth stages, but has broad, low ribs on which all tubercles are very much reduced at maturity. We figure here an undescribed American form from New Mexico which shows it to have had constricted inner whorls, thus confirming the close affinity (text-fig. 2).



TEXT-FIG. 2. *Shuparoceras* sp. nov. Plaster cast of a specimen (15947) in the U.S. Geological Survey Collections, Denver, from the mid Turonian *Prionocyclus hyatti* Zone, 46 km north-west of Albuquerque, New Mexico. Specimen shows inner whorls with constrictions, and the distinctive feebly ornamented outer whorls of the genus. (Courtesy of W. A. Cobban, Denver.)

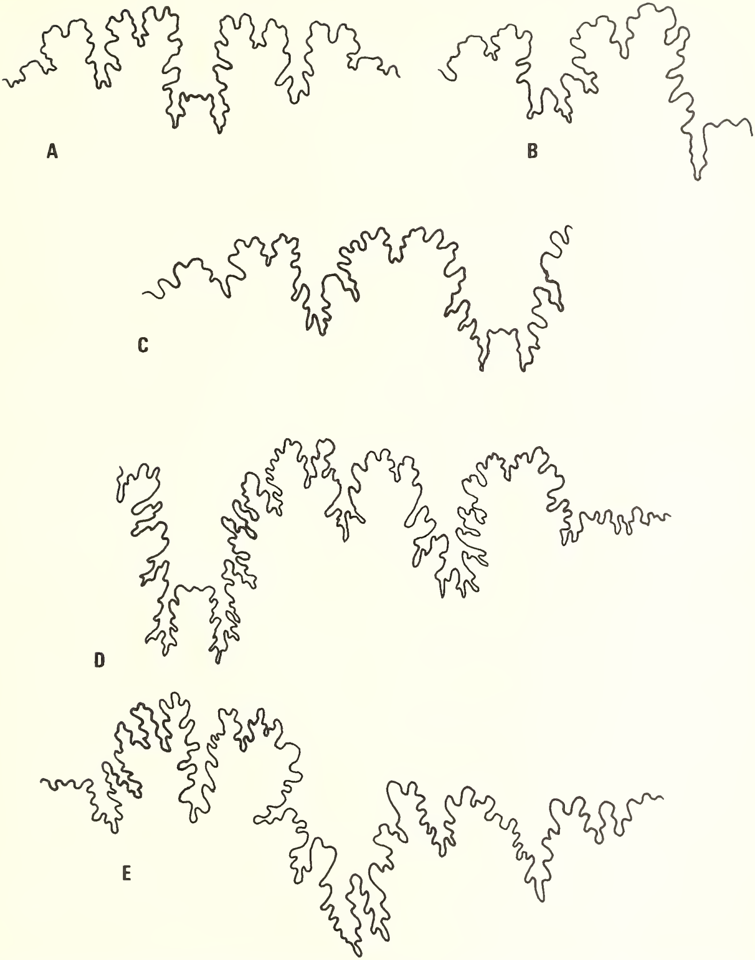
Kamerunoceras Reyment, 1954 (type species *Acanthoceras eschii* Solger, 1904, p. 124, pl. 4, figs. 1-4) are typically very evolute, slowly expanding, and almost serpenticone with a polygonal whorl section; they either lack a mid-lateral tubercle, having only seven rows in all (as in the type species), or the tubercle in this position is an umbilical one which has migrated outwards during ontogeny. Furthermore, the siphuncle lies close to the surface producing a low rounded siphonal ridge. The number of siphonal tubercles may exceed the ventral, and ventral ribbing tends to be irregular in many species. We regard *Schindewolfites* Wiedmann, 1960 as a synonym of *Kamerunoceras* (see Kennedy and Wright 1979).

Less readily resolved is the relationship between *Romaniceras* and the poorly known *Tunesites* Pervinquière, 1907. The type species of this genus, *T. salammbo* Pervinquière (1907, p. 255, pl. 12, figs. 5*a-b*, 6*a-b*; text-fig. 101) is based on a pyritic nucleus from the 'Cénomanien ou, à la rigueur, du Gault supérieur du Dj. Guern Halfaya pied N-W, non loin d'Henchir er Ressas', Tunisia. The specimen, refigured here as Pl. 39, figs. 19-23, is only 16 mm in diameter but exquisitely preserved. Its inner whorls are smooth, evolute, with a compressed, rounded whorl, but at approximately 8 mm diameter a strong prorsiradiate constriction develops, flanked by distinct collar-ribs. There are three such constrictions on the outer whorl, with progressively stronger collars, and low, irregular ribs develop on the flanks between constrictions, with progressively stronger and more numerous obliquely placed ventral tubercles developing as size increases. The venter changes from rounded to weakly fastigiate from the second constriction, with the development of a low siphonal ridge. Low ribs form a chevron linking the ventral tubercles to this ridge, with siphonal clavi developed at the peak of the chevron on the ridge. The suture line (text-fig. 3A) includes broad, little incised saddles and much narrower lobes. *T. choffati* Pervinquière (1907, p. 257, pl. 12, figs. 7*a-b*, 8*a-b*; text-fig. 102; see Pl. 39, figs. 11-16; text-fig. 3B) has, as Pervinquière noted (1907, p. 257), identical innermost whorls, and he thought that perhaps they represented no more than variants of one species. The chief differences are *T. choffati*'s much earlier acquisition of constrictions and associated collars and much stronger flank ribs between, even at an early stage. The smaller paratype (Pl. 39, figs. 11-14) shows no trace of ribs or tubercles on the venter. In contrast, the larger holotype (Pl. 39, figs. 15-16) has flexuous primary ribs which sweep forwards across the venter at only 10 mm diameter and rapidly develop umbilical bullae, conical inner and outer ventrolateral and clavate siphonal tubercles borne on what are exclusively primary ribs; a radially elongate lateral tubercle appears at a somewhat greater diameter. The suture differs from that of the type *T. salammbo* (text-fig. 3B) in having a broader and deeper L. Unlike the poorly dated type of *T. salammbo*, this species, which comes from Koudiat el Hamra, is from a level, 'sensiblement au niveau de *Forbes. obtectum*'—that is to say probably Middle Cenomanian. The smaller paratype is from A. ez Zerga, '*mais son étiquette indique le Turonien* (*avec un point d'interrogation*' (our italics).

Only Pervinquière's labels now survive with these specimens, but it appears that he may not himself have collected them, for as he indicates in the introduction to his memoir, he was given many specimens by Flick, Thomas, and Peron to use in his work. We would therefore conclude that all these specimens, dated as anything from Albian to Turonian, cannot all be accepted as definitely Cenomanian.

The holotype of *T. salammbo*, with only ventrolateral and siphonal tubercles developed, could be the nucleus of a *Hourcquiceras* Collignon, 1939 (see, e.g., Pl. 39, fig. 24); or a *Kamerunoceras* (see, e.g., Solger 1904, p. 124, pl. 4, figs. 1-4), the nucleus of the type specimen of the type species of which is smooth and round-whorled and develops one constriction with feeble collars at a similar size to *T. salammbo*; or a *R.* (*Romaniceras*) (e.g. Pl. 39, figs. 7-10) or a *R.* (*Yubariceras*) (e.g. Pl. 40, fig. 1). In contrast, *Euomphaloceras* is already strongly ribbed and tuberculate at this size. It is therefore clear that *Tunesites* must be treated as a *nomen dubium* since the type is too small to be generically determinable. In contrast, the holotype of *T. choffati*, with its full complement of umbilical, lateral, inner and outer ventrolateral and siphonal tubercles, is a *R.* (*Romaniceras*), and probably *R.* (*R.*) *deverianum*.

That this circuitous elimination of *Tunesites* is not mere special pleading is confirmed by the recognition that *Eucalycoceras constrictum* Spath, 1926 (= *Acanthoceras* aff. *A. Newboldi* Kossmat



TEXT-FIG. 3. External sutures of *Tunesites* and *Romaniceras*. A. *Tunesites salammbo* (Pervinquière); holotype, ×6. B. *Tunesites choffati* (Pervinquière); holotype, ×6. C. *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka); GK H5685, ×3. D. *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny); the lectotype of *Ammonites medlicottianus* Stoliczka. ×1. E. *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka); the holotype, ×1. (A–B, after Pervinquière, 1907; C, after Matsumoto, 1975; D, E, after Stoliczka, 1865).

of Pervinquière, 1910, p. 45, pl. 4, fig. 37), based on a small pyritic specimen in the Peron collection (but collected by Thomas) and said to be from the Middle Cenomanian of Berrouaghia, Algeria, is also a *R. deverianum* (Pl. 39, figs. 7–10). It has a smooth, constricted initial stage with collars, then develops flexuous long ribs with a full complement of nine rows of tubercles over the last half-whorl. The intermediate stage, although crushed and distorted, shows umbilical bullae and ventral tubercles to be the first to develop, with a broad, smooth venter, in contrast to the early appearance of siphonal tubercles in *T. salammbo*.

Occurrence. The main occurrence of *Romaniceras* is in the middle part of the Turonian stage; the earliest dated occurrence known to us is in the St. Cyr-en-Bourg Fossil Bed of Touraine (Hancock, Kennedy, and Wright 1977). It also extends to the upper Turonian in Japan. The geographic distribution includes England and France, Czechoslovakia (Bohemia), the Middle East (Israel, Lebanon), Algeria, Tunisia, Nigeria, Madagascar, southern India, Japan, British Columbia, Oregon, California, the western interior of the United States, Texas, and Mexico.

Subgenus *Romaniceras* (*Romaniceras*) Spath, 1923
[= *Proromaniceras* Wiedmann, 1960]
Romaniceras (*Romaniceras*) *deverianum* d'Orbigny

Pl. 39, figs. 7–10; Pl. 41, figs. 1–6; Pl. 42, figs. 1–7; Pl. 43, figs. 1–3; text-figs. 1, 3D, 4, 5

1841 *Ammonites deverianus* d'Orbigny, p. 346, pl. 110, figs. 1–2.
1850 *Ammonites Deverianus* d'Orbigny, p. 189.
1857 *Ammonites deverianus* d'Orbigny; Sharpe, p. 43, pl. 19, fig. 5*a*–*b*.
1865 *Ammonites medlicottianus* Stoliczka, p. 77, pl. 43, fig. 1–1*b*.
1872 *Ammonites Deverianus* d'Orbigny; Fritsch, p. 32, pl. 7, figs. 4–5.
1894 *Acanthoceras pseudodeverianum* Jimbo, p. 178, pl. 21, fig. 1–1*b*.
1897 *Acanthoceras Medlicottianum* Stoliczka; Kossmat, p. 16.
?1907 *Tunesites Choffati* Pervinquière, p. 257, pl. 12, figs. 7*a*–*b*, 8*a*–*b*; text-fig. 102.
1910 *Acanthoceras* aff. *A. Newboldi* Kossmat; Pervinquière, p. 45, pl. 4, fig. 37.
1913 *Acanthoceras deverianum* d'Orbigny; Roman and Mazeran, p. 25, pl. 3, figs. 1, 1*a*, 2, 2*a*; ? text-fig. 4.
1923 *Ammonites deverianus* d'Orbigny; Spath, p. 144.
1926 *Eucalycoceras constrictum* Spath, p. 431.
non 1937 *Acanthoceras deverianum* Basse, *non* d'Orbigny, p. 180, pl. 8, figs. 1*a*–*b*, 2*a*–*b* (= *R.* (*Y.*) *ornatissimum* (Stoliczka)).
1939 *Romaniceras deveriai* d'Orbigny; Collignon, p. 93, pl. 8, figs. 2, 3–3*a*; pl. 9, fig. 1–1*a*.
1939 *Romaniceras deveriai* d'Orbigny var. *masiaposensis* Collignon, p. 89, pl. 9, figs. 2, 2*a*–*b*.

EXPLANATION OF PLATE 39

All figures are × 2.

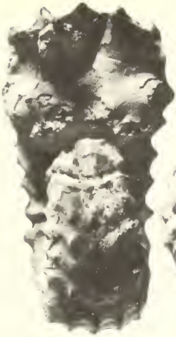
Figs. 1–6, 17–18. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). Early developmental stages of OUM KT 993 from the mid Turonian of Swede Creek, Shasta County, California (ex W. P. Popenoe collection).

Figs. 7–10. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). The holotype of *Eucalycoceras constrictum* Spath, 1926 (= *Acanthoceras* aff. *A. newboldi* Kossmat of Pervinquière, 1911 p. 45, pl. 4, fig. 37). Said to be from Berrouaghia, Algeria (Sorbonne collections).

Figs. 11–16. *Tunesites choffati* Pervinquière. 11–14 paratype from A. ez Zerga; 15–16 holotype, from Koudiat el Hamra, Tunisia (Sorbonne collections).

Figs. 19–23. *Tunesites salammbo* Pervinquière. Holotype, from Djebel Guern Halfaya, Tunisia (Sorbonne collections).

Fig. 23. *Hourcquiceras hourcqi* Collignon. Inner whorls of a specimen from the late Cenomanian of Ankilimanarivo, Madagascar, in C. W. Wright's collection.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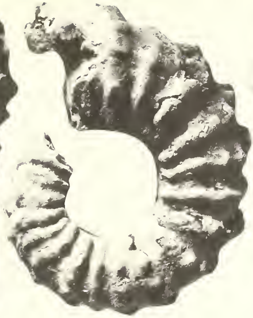
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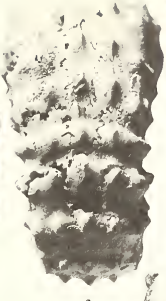
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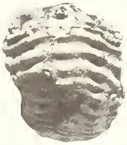
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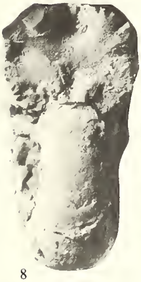
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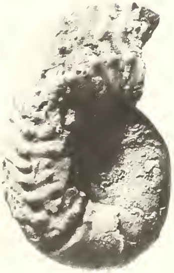
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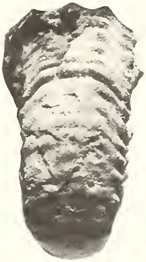
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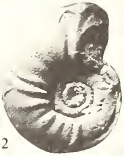
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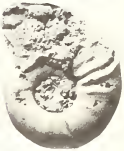
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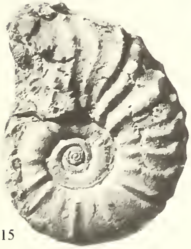
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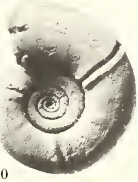
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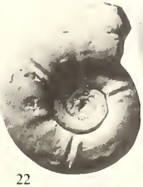
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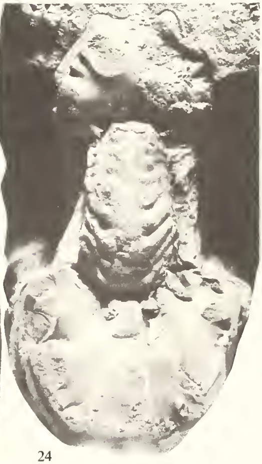
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KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

1939 *Romaniceras uchauxiense* Collignon, pp. 89, 94, pl. 10, fig. 1, 1*a*.
1951 *Romaniceras* sp., Wright and Wright, p. 29 (*pars*).
1957 *Romaniceras* aff. *uchauxiense* Collignon; Matsumoto, Saito and Fukada, p. 24, pl. 9, figs. 1*a–c*, 2; pl. 14, fig. 1*a–b*; pl. 15, fig. 2.
1957 *Romaniceras pseudodeverianum* (Jimbo); Matsumoto, Saito and Fukada, p. 22, pl. 8, fig. 3; text-fig. 7*a–d*.
?1957 *Romaniceras* (?) otatumei Matsumoto, Saito, and Fukada, p. 25, pl. 2, fig. 2*a–b*.
1958 *Acanthoceras sharpei* Zázvorka, p. 43 (pars.), pl. 2, figs. 3–4 (non 5).
1958 *Acanthoceras deverianum* (d'Orbigny); Zázvorka, pl. 1, figs. 1, 2.
?1959 *Romaniceras* aff. *pseudodeverianum* (Jimbo); Matsumoto, p. 92, pl. 27, fig. 1*a–b*; text-fig. 46.
1965 *Romaniceras deveriai* d'Orbigny; Collignon, p. 22, pl. 384, fig. 1655.
1965 *Romaniceras uchauxiense* Collignon; Collignon, p. 22, pl. 384, fig. 1656.
?1969 *Romaniceras deverianum* (d'Orbigny); Freund and Raab, p. 6.
1975 *Romaniceras* sp. aff. *R. deverianum* (d'Orbigny); Matsumoto, p. 117, pl. 14, fig. 1*a–c*.
1975 *Romaniceras yezoense* Matsumoto, p. 118, pl. 14, fig. 2; pl. 15, figs. 1*a–b*; text-figs. 5–6.
?1975 *Yubariceras otatumei* (Matsumoto, Saito and Fukada); Matsumoto, p. 144, pl. 21, fig. 1*a–c*; text-figs. 15–16.

Types. The problems associated with the type material are discussed above (p. 327).

Specimens studied. From Uchaux, Vaucluse: MNHP 6781 (d'Orbigny collection), a syntype; EMP, Fontannes collection, a silicified juvenile 83·4 mm in diameter. MNHP, Peron collection (unregistered), two juveniles, 40 and 80 mm in diameter. MNHP, two partially silicified adults collected by Dr. J. Sornay. FSL 14210 (the holotype of *R.* (*R.*) *uchauxiense*), 13695.

An unregistered specimen in the MNHP, labelled Faluns de Touraine, and in a Tuffeau Preservation. From the Tuffeau Jaune of Touraine: casts of two specimens (MNHP, LC) Biet collection, from Nouans (Indre et Loire); SP—an unregistered specimen labelled '*Ammonites*' Craie de Touraine (Z. à *Callianassa archiaci*) St. Georges sur Cher?, M. Heb. [ert?] 61-624. LC 417BAc, labelled Beidoze, Les Ranges; ?LC (Reignoux collection), unregistered and unlocalized; ?LC unregistered, Carrière du Riveau, Grand Pressigny; LC unregistered, Montlouis-sur-Loire, La Barre; LC unregistered, Loches (l'Etang). The holotype of *Romaniceras sharpei* (Zázvorka), BMNH C 34596 (= Sharpe 1857, p. 46, pl. 19, fig. 5*a–b*), from the Middle Chalk of Sussex. BMNH C 34946, from the *Terebratulina lata* Zone Middle Chalk of Amberley, Sussex; WW 22746 from 2 m below the Chalk Rock at Latimer, Buckinghamshire.

From southern India we have seen a fine topotype of *Ammonites medlicottianus* Stoliczka from Odium in the collections of the Naturhistorisches Museum, Vienna. We have also examined all the Japanese material listed in the synonymy.

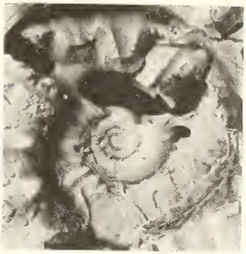
The holotype, and only specimen, of *Eucalycoceras constrictum*, which forms the basis of the description of the earliest stages of the species, is in the collections of the Sorbonne. The specimen was collected by P. Thomas and recorded as coming from the middle of his second zone of the Cenomanian at Berrouaghia. In spite of this apparently exact record, the association listed by Pervinquière (1910, p. 78) indicates more than one horizon, and the specimen is unlike any known Cenomanian ammonite. We know from our own field-work that around Berrouaghia the Turonian also yields limonitic nuclei of ammonites.

EXPLANATION OF PLATE 40

Fig. 1 is × 2; the remainder are × 1.

Figs. 1, 3–5. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). 1, inner whorls of GK H5685, from the *Inoceramus hobetsensis* Zone, Hobetsu area, Kyushu, Japan. 3–5, the holotype of *Yubariceras yubarense* Matsumoto, Saito, and Fukada, UT MM7620 (= 1–343) from a pebble in the bed of the Pankemoyuparo, near the mouth of the Kaneobetsu, Oyubari area, Kyushu, Japan.

Figs. 2, 6. *R.* (*Obiraceras*) *ornatum* Matsumoto. Holotype, GK H5689, from the Upper Turonian of Sato-no-sawa, Obira area, Hokkaido.



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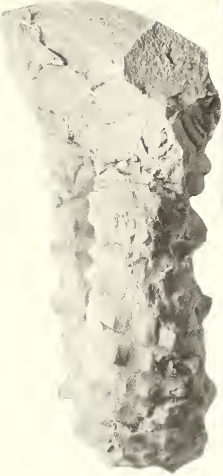

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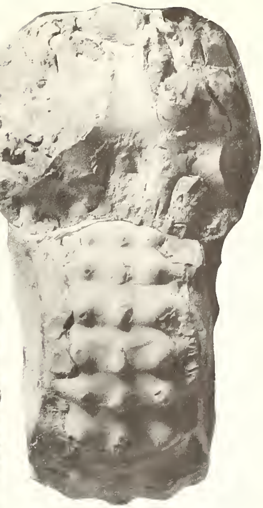

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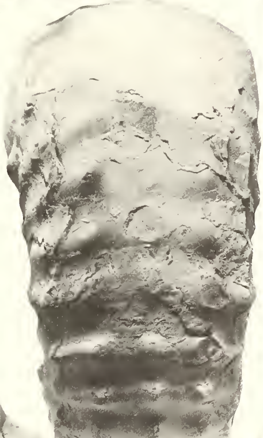

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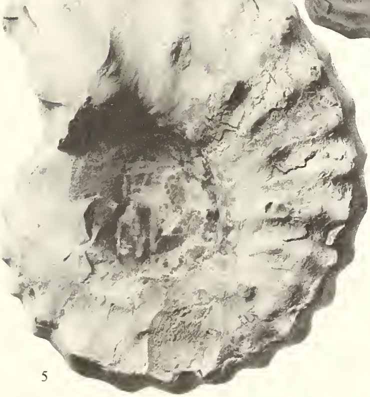

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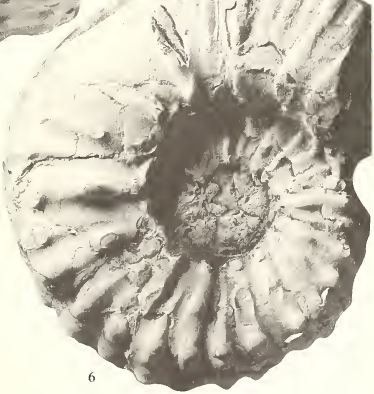


6

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Dimensions	*D*	*Wb*	*Wh*	*Wb:Wh*	*U*	*Ribs*
d'Orbigny's original figures	94·0(100)	44·0(47)	39·0(42)	1·13	29(31)	36/37
Holotype of *R.* (*R.*) *pseudodeverianum* (after Matsumoto *et al.*)	195·0(100)	—(—)	75·0(38)	—	68·5(35)	32
Holotype of *R.* (*R.*) *uchauxiense*	147·5(100)	58·5(40)	68·5(46)	0.85	39·5(27)	31/32
Holotype of *R.* (*R.*) *yezoense* (after Matsumoto)	218(100)	76·0(35)	95·0(43)	0·8	58·0(26)	37
Lectotype of *R.* (*R.*) *medlicottianum* (from the figure)	215(100)	97·45	90(42)	1·1	75(35)	23
EMP, coll. Fontannes	83·4(100)	—(—)	39·0(47)	—	25·0(30)	41/42
	76·7(100)	28·0(37)	36·5(48)	0·78	22·7(30)	41/42
MNHP, coll. Peron (distorted)	64·5(100)	31·0(48)	32·5(50)	0·95	15·0(23)	32

Description. The very earliest stages with constrictions are known only from the imperfectly preserved and distorted holotype of *E. constrictum* Spath (Pl. 39, figs. 7–10). The nucleus up to a diameter of 5·5 mm appears to have been evolute, with a depressed, rounded whorl, lacking ornament, so far as is visible. On the outer whorl beyond a diameter of 5·5 mm the earliest ornament to appear is in the form of low, broad, distant ribs, arising as weak bullae, passing forwards across the flank and weakening on the venter which they cross with a broad convexity accompanied, possibly, by weak intercalated ribs. There are initially neither tubercles nor constrictions, but a relatively large clavate ventrolateral tubercle is present at a position 270° back from the end of the specimen (approximately 10 mm diameter), and two strong, slightly flexed, prorsiradiate constrictions are developed in the next 90° (Pl. 39, fig. 9). The collar ribs of the first constriction bear umbilical bullae and a ventral node as the only obvious tubercles (although preservation is poor). Those of the second are stronger and bear strong umbilical bullae projected into the umbilicus, conical inner lateral, bullate inner and outer ventrolateral, and a suggestion of a transverse siphonal tubercle. The remainder of the specimen to a (deformed) diameter of 23 mm develops a markedly octagonal, depressed whorl section, with numerous crowded, feebly flexuous ribs, strongly projected forwards across the ventrolateral shoulder but crossing the venter with only a shallow convexity. There are nine rows of tubercles, as noted above, which become progressively stronger as size increases, the siphonal row initially the weakest, the inner ventrolateral, outer ventrolateral, and siphonal rows markedly bullate.

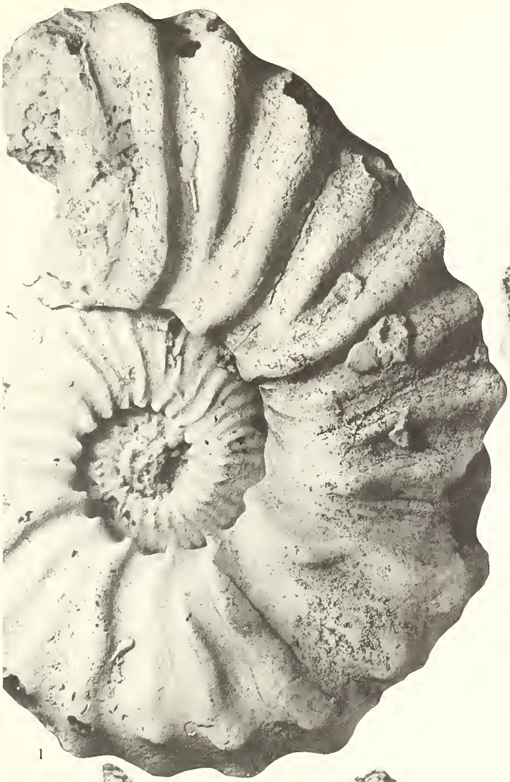
The smallest topotypes before us are 40–50 mm in diameter (Pl. 41, figs. 5, 6) and, like most Uchaux specimens, retain silicified shell. These, like the dorsum of one of the Sornay specimens, show the same style of ribbing and constrictions seen in *E. constrictum*.

Coiling is relatively evolute in middle and later growth, the whorl section varies from slightly depressed to compressed (Wb:Wh = 0·78–1·13) and is polygonal, with the greatest breadth at the lateral tubercle. There is a total of 32 to 42 ribs per whorl, the density increasing with whorl-compression. Most ribs arise from umbilical bullae; a few are intercalated low on the flank or extend from the umbilicus without a bulla. Periodically ribs bifurcate from the lateral tubercle. In depressed individuals the ribs are straight and recti- to prorsiradiate; in compressed ones they may be gently flexed (Pl. 42, fig. 1). The umbilical bullae project into the umbilicus and in well-preserved individuals become subspinate, resembling in this respect the Cenomanian *E. gothicum* (Kossmat) (1895, p. 69, pl. 25, fig. 3*a*–*c*). There are well-developed, more or less bullate, lateral tubercles, conical inner ventrolateral, subequal outer ventrolateral, and siphonal tubercles, rounded on moulds and conical on depressed individuals with shell preserved but all clavate in compressed ones. In these latter the clavi form semi-continuous nodose ridges in some specimens when covered by a dorsal callus (Pl. 42, fig. 2). Well-developed constrictions, parallel to the ribs, are visible on several nuclei up to diameters of at least 30 mm.

As size increases beyond about 70 mm, ribs typically broaden and coarsen and the lateral tubercles may weaken. There is a tendency for long and short ribs to alternate regularly, ribs to become more widely spaced on

EXPLANATION OF PLATE 41

Figs. 1–6. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). 1–2, MNHP unregistered (Sornay collection). 3–4, MNHP 6781 (d'Orbigny collection), the surviving syntype. 5–6, MNHP, Peron collection. All specimens are silicified, and from Uchaux, Vaucluse. 1–2 are reduced × 0·8; the remainder are × 1.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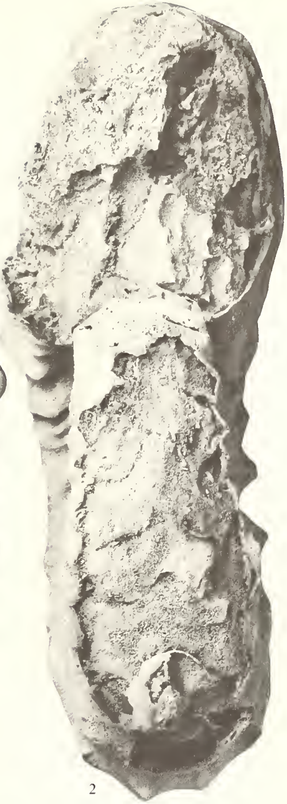
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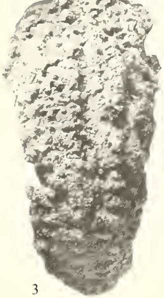
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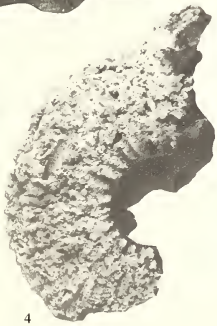
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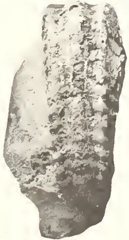
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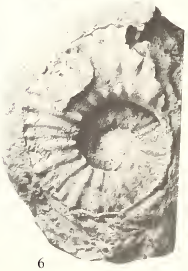
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KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

the venter and outer ventrolateral and siphonal clavi to elongate markedly. The largest specimens we have seen tend to become high-whorled, and even those with depressed inner whorls and rounded ventral tubercles show this feature (see, e.g., Collignon 1939, pl. 8, fig. 2; pl. 9, fig. 1*a*).

None of the topotype specimens before us shows the suture line.

Discussion. The inflated Uchaux specimens, such as the syntype in the d'Orbigny collection and that figured by Roman and Mazeran (1913, pl. 41, fig. 2, 2*a*), occur with more compressed individuals which develop long, high, *Barroisiceras*-like ventral and siphonal clavi at maturity. Collignon (1939, p. 37) named these *R. uchauxiense*, and subsequent authors have maintained the two species as separate. Both types show the same arrangement of tubercles and both have the characteristic spinate umbilical bulla projecting into the umbilicus. Forms of intermediate inflation are present (Pl. 42, figs. 4, 7). The strongly clavate ventral and siphonal tubercles are a feature of the later growth stages, and even the compressed and densely ribbed individual shown in Pl. 42, figs. 1-3, has the characteristic clavate outer ventrolateral and rounded siphonal tubercles of typical *R. deverianum*. We would also note that the type of *R. uchauxiense* is extreme in its ventral decoration even by comparison with other specimens referred to the species and shows signs of pathological disturbance which have accentuated these features. All the Uchaux specimens share details of ornament and development in common, upon which is expressed a covariance in ribbing style and density linked to a compressed, versus depressed, whorl, as is widely demonstrated in acanthoceratids. In terms of the *Acanthoceras rhotomagense* population described by Kennedy and Hancock (1970), *deverianum* corresponds to *rhotomagense sussexiense* and *uchauxiense* to *rhotomagense clavatum*. The two occur together wherever any numbers of specimens are known, as in Touraine, Japan, and Madagascar, in addition to Uchaux.

Interpreted in this way, a number of other species, we believe, fall into the synonymy of *R. deverianum*. The earliest described of these is *Ammonites medlicottianus* Stoliczka (1865, p. 77, pl. 43, fig. 1*a–c*) from the Uttatur Group north of Odium, southern India. The species is based on several specimens; that illustrated by Stoliczka is here designated the lectotype. We have fortunately been able to study a large topotype in the collections of the Naturhistorisches Museum, Vienna. These specimens show an intermediate degree of inflation and rib density between comparably sized individuals referred by previous authors to *deverianum* and *uchauxiense*, in particular resembling the cast of the larger of the Nouans specimens before us, especially in ventral aspect, but retaining a stronger lateral tubercle. Its inner whorls are relatively finely ribbed compared with the outer, like those of the Madagascan example figured by Collignon (1965, pl. 384, fig. 655); these appear to be differences of individual, rather than specific significance, although we do not know the full range of variation of the Indian population.

R. pseudodeverianum Jimbo (1894, p. 178, pl. 21, fig. 1-1*b*; see also Matsumoto, Saito and Fukada 1957, p. 22, pl. 8, fig. 3; text-fig. 7A–D) is a Japanese species based on a single specimen (GT. I-106) collected loose in the bed of the Obirashibets River, Teshio Province, Hokkaido; it was made the type species of the subgenus *Proromaniceras* Wiedmann, 1960. All of one side of the type specimen is worn away and previous reconstructions of the whorl section (Matsumoto *et al.* 1957, text-fig. 7A–D) are schematic. Furthermore, almost all of the venter and most of the flank of the outer whorl of the preserved side is waterworn (Pl. 43, figs. 1-3), so that ribs on the last half-whorl are unnaturally weak. The specimen bears bullate umbilical tubercles, strong bullate laterals, and conical to bullate inner ventrolateral tubercles. The outer ventrolateral tubercles are worn but appear to have been strong

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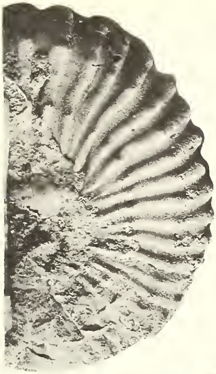
EXPLANATION OF PLATE 42

Figs. 1-7. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). 1-3, FSL 13965. 4, 7, MNHP, Peron collection. 6, MNHP 1904-32; all specimens silicified, and from Uchaux, Vaucluse. 5, the holotype of *Eucalycoceras constrictum* Spath. See explanation of Plate 1, figs. 7-10 for details. Fig. 5 is ×2; the remainder are ×1.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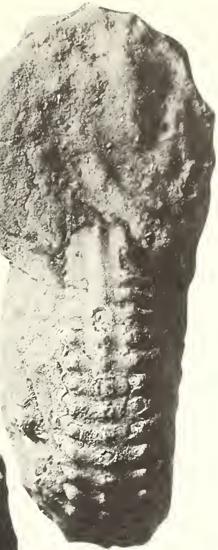
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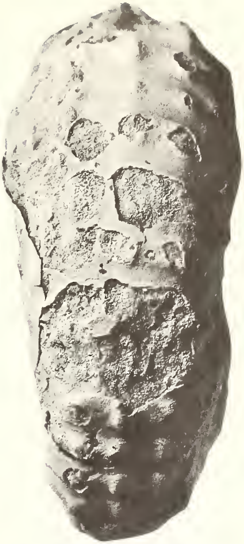
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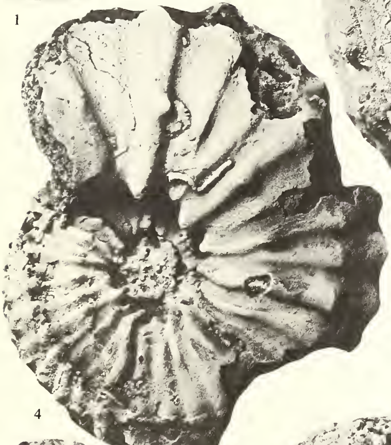
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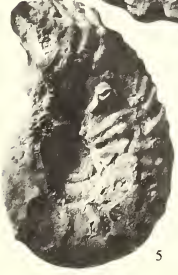
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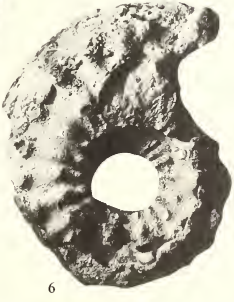
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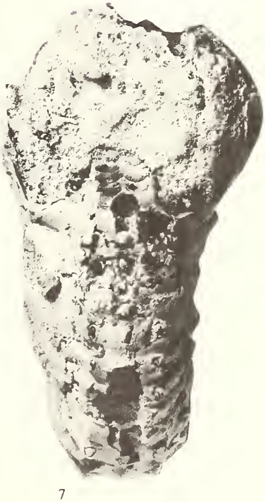
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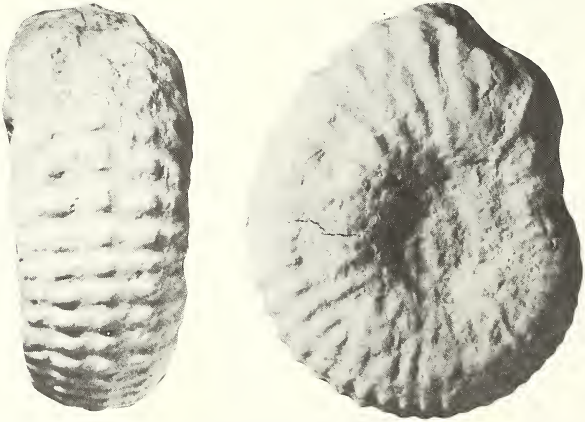
KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

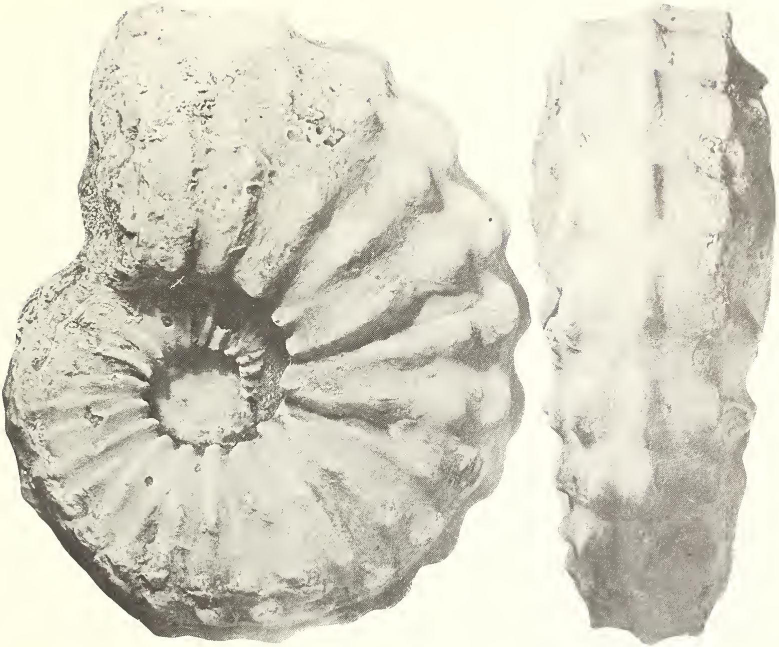
and slightly clavate; the siphonal tubercles are weaker and clavate. There is branching and intercalation of ribs at the smallest diameter visible, but on the last half-whorl most of the ribs are long and are crowded, suggesting that this is a small adult. The type of *R. pseudodeverianum* has the strong ribs of d'Orbigny's protograph, but within the limits of preservation the lateral tubercle appears to remain rather low on the flank throughout growth. As for the ventral tubercles of the last half whorl, both the inner and outer ventrolaterals appear transversely rather than spirally elongate and are in the process of assimilation into a ribbed mature body-chamber ornament. These differences seem to be no more than of individual significance. *Acanthoceras sharpei* Zázvorka (1958, p. 43) was based on Sharpe's specimen (1857, p. 43, pl. 19, fig. 5*a–b*) of *deverianum*. This (BMNH 34549) has a compressed, flat-sided, whorl section and is more densely ribbed than d'Orbigny's protograph, but corresponds at a similar size to the smaller of the specimens from Nouans (text-fig. 4).

R. kallesi (Zázvorka) (1958, p. 39; text-fig. 1, figs. 1–2) is a distinct, early species of *R.* (*Romaniceras*) discussed further below. Features which separate it from *R.* (*R.*) *deverianum* at a comparable degree of inflation are the rectangular whorl section, lower expansion rate, evolute coiling, and weaker tuberculation, especially in the umbilical bullae; the weak lateral tubercles are low on the flank and are rapidly lost; interspaces are wide on the venter. The species is adult at a much smaller size than *R. deverianum* and none of the specimens of *R. kallesi* before us approach the inflated whorl section and strong lateral tuberculation of typical *deverianum*, nor do they show the compression and clavate ventrolateral tubercles of the slender *uchauxiense* type.

Of the north African forms, *E. constrictum* Spath has already been shown to be based on a juvenile *R. deverianum* (p. 332). *Tunesites choffati* Pervinquière (Pl. 39, figs. 11–16) is also a juvenile *R.* (*Romaniceras*). The smaller paratype has much stronger ribs on the untuberculate constricted portion and in this respect differs from what we have taken as a *R. deverianum* nucleus (Pl. 39, figs. 7–10); it is specifically indeterminate in our present state of knowledge. The larger holotype is unfortunately crushed but resembles closely the inner whorls of the Uchaux specimen shown as



TEXT-FIG. 4. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). Plaster cast of a juvenile specimen (EMP, LC), Biet Collection, from the Tuffeau Jaune de Touraine of Nouans, Indre-et-Loire.



TEXT-FIG. 5. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). Plaster cast of the holotype of *R.* (*Romaniceras*) *uchauxiense* Collignon, FSL 13964, from Uchaux, Vaucluse. Reduced × 0·8 approx.

Pl. 41, figs. 5–6; it too may thus be a synonym of *R. deverianum*, in spite of the obvious differences from the type of *E. constrictum*.

R. (*R.*) *otatumei* Matsumoto, Saito and Fukada (1957, p. 25, pl. 2, fig. 2; Matsumoto 1975, p. 144, pl. 21, fig. 1; text-figs. 15–16) is a further species based on a juvenile which may be within the range of *R. deverianum*, having, however, much stronger lateral tubercles on some ribs. It resembles the type of *T. choffati* at the same size.

Yubariceras japonicum Matsumoto, Saito and Fukada (1957, p. 31, pl. 8, fig. 2; text-figs. 11, 12; Matsumoto 1975, p. 139, pl. 19, figs. 2–3; pl. 21, fig. 2; text-figs. 13–14) has only nine rows of tubercles and is a typical *R.* (*Romaniceras*). It appears to be one of those passage forms of intermediate inflation that compares with the Uchaux specimen shown in Pl. 42, fig. 2, even to the point of having the same dorsal callosity.

'*Yubariceras*' aff. *japonicum* of Matsumoto (1975, p. 143, pl. 21, figs. 3–4; pl. 23, fig. 2) has parallel flanks, a rounded venter, distantly spaced, low, flexuous, prorsiradiate ribs and bullate lateral tubercles quite close to the umbilical; it is quite distinct from any European specimen we have seen.

'*Y.*' *pseudomphalum* Matsumoto (1975, p. 146, pl. 22, fig. 1) is based on a single specimen from the Oyubari area of Hokkaido. It has nine rows of tubercles but differs from *R. deverianum* in its depressed whorl section and primary ribs, differentiated into relatively weak and relatively strong with intercalated ventral ribs on the phragmocone but all the body-chamber ribs long. This *Euomphaloceras*-like form is quite distinctive.

'*Y.*' *fujishimai* Matsumoto (1975, p. 148, pl. 22, fig. 2; pl. 23, fig. 3; text-fig. 17) has nine rows of tubercles and is also based on a single specimen from the Oyubari area of Hokkaido. Like *R. pseudomphalum* (from which it may not be specifically separate) it has intercalated *Euomphaloceras*-like ventral ribs and tubercles which immediately distinguish it from *R. deverianum*.

The *Romaniceras* described from Mexico by Jones (1938) are in part *Shuparoceras* (e.g. *R. indiduraense* Jones, p. 119, pl. 7, figs. 2–4; and perhaps '*Romaniceras*' *santaanaense* Jones, p. 121, pl. 8, figs. 1, 6). *Romaniceras kanei* Jones (1938, p. 120) is a *R.* (*Yubariceras*). The types of *R. adkinsi* Jones (1938, p. 120, pl. 8, figs. 4, 5) and *R. mexicanum* Jones (1938, p. 121, pl. 7, figs. 1, 6) are so poor that the species should be treated as *nomina dubia*. They differ from *R. deverianum* in having massive whorls with broad, flattened venters. *R.* (?) *coahuilaense* Jones (1938, p. 118, pl. 6, fig. 1; pl. 8, fig. 5), which may be similarly separated, is coarsely and grossly ribbed and tuberculate. *R. toribioense* Jones (1938, p. 122, pl. 7, figs. 7–8) is based on a very poor fragment and although it might be a part of a slender *R. deverianum* is best treated as generically indeterminate. The *R. uchauxiense* of Reyment (1955, p. 46, pl. 9, fig. 2) shows doubling of the ventral tubercles and appears to be a fragment of an *Obiraceras*.

Occurrence. *R.* (*R.*) *deverianum* is a late mid Turonian species known from southern England, Touraine and Vaucluse in France, Bohemia, Algeria, Tunisia (?), Israel (?), Madagascar, southern India, and Japan.

Romaniceras (*Romaniceras*) *kallesi* (Zázvorka, 1958)

Pl. 44, figs. 1–3; Pl. 45, figs. 2–7; Pl. 46, figs. 1–4; Pl. 47, figs. 1–4; text-fig. 6

1958 *Acanthoceras kallesi* Zázvorka, p. 39, pl. 1, figs. 1–2.
1958 *Acanthoceras*, Zázvorka pl. 2, fig. 5 only.
1960 *Romaniceras* (*Proromaniceras*) *pseudodeverianum hispanicum* Wiedmann, p. 735, pl. 2, figs. 3, 4.
1964 *Romaniceras* (*Proromaniceras*) *pseudodeverianum hispanicum* Wiedmann, p. 123, text-fig. 4*a*–*b*.
1977 *Romaniceras hispanicum* Wiedmann; Hancock, Kennedy, and Wright, pp. 156 et seq.

Types. The holotype is the original of Zázvorka 1958, pl. 1, fig. 1, no. 36938, and the paratype no. 2119, the original of his pl. 1, fig. 2, both from the Turonian Spongolith facies of the White Mountain near Prague, Czechoslovakia.

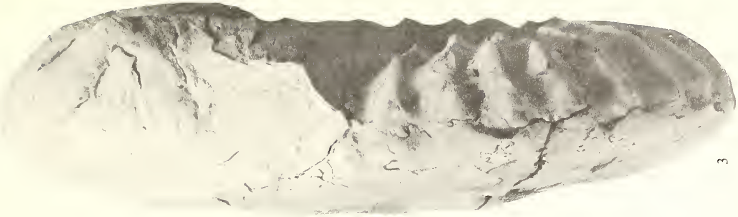
Material studied. Casts and photographs of the holotype of *Romaniceras kallesi*, supplied through the courtesy of Drs. R. Zázvorka and V. Houša, plus a cast of a topotype in the British Museum (Natural History) no. 88992.

Specimens in the Muséum d'Histoire Naturelle, Angers, are: AM 18, 34a–b, 35, from St Cyr-en-Bourg; AM 47, from Saumoussay; AM 45, 114, 115, from Saumur; AM 33 from Montsoreau, and AM 119–120 from Chateauneuf-sur-Loir. A fine unregistered specimen in the collections at Nantes is simply labelled 'Touraine'. OUM KZ755–757 collected by us from the St Cyr-en-Bourg Fossil Bed, Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine et Loire.

Through the courtesy of Professor Dr. J. Wiedmann (Tübingen) we have also been able to study a cast of the holotype of *R.* (*R.*) *hispanicum*.

EXPLANATION OF PLATE 43

Figs. 1–3. *R.* (*Romaniceras*) *deverianum* (d'Orbigny). The holotype of *Acanthoceras pseudodeverianum* Jimbo, the type species of *Proromaniceras* Wiedmann, 1960. This badly worn specimen, GT 1-106 (=MM7516) is from a boulder in the bed of the Opirashibets, Teshio Province, Hokkaido, Japan. Reduced ×0·7.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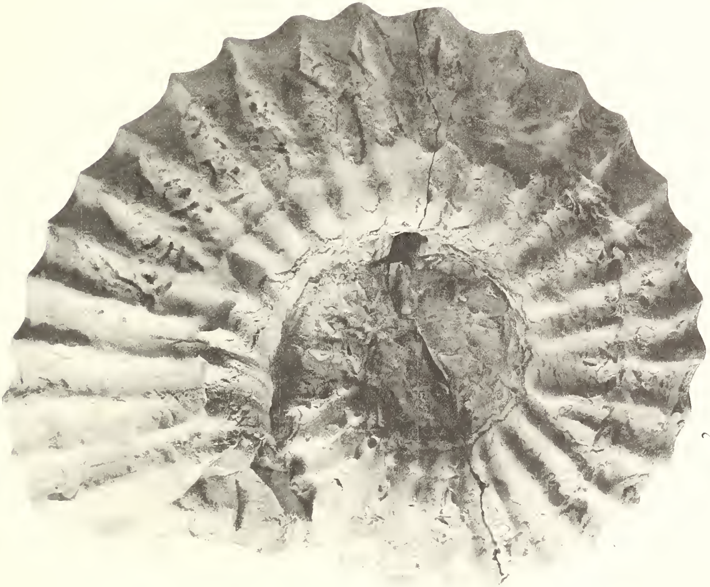
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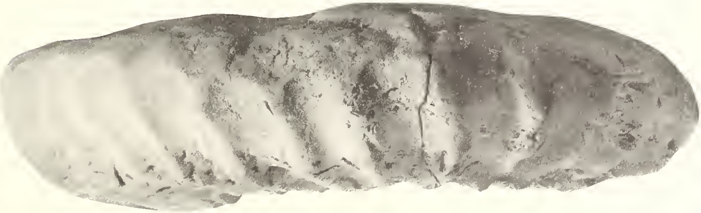
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KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Dimensions	*D*	*Wb*	*Wh*	*Wb:Wh*	*U*	*R*
Nantes specimen	141·0(100)	48·5(34)	54·5(39)	0·9	53·0(38)	43
AM 114	97·5(100)	40·0(41)	39·0(40)	1·0	33·0(34)	41
AM 34*a*	146·0(100)	53·0(36)	54·0(37)	0·98	52·0(36)	35
AM 35	114·0(100)	47·0(41)	50·0(44)	0·94	37·0(32)	—

Description. This is a rather small species, adult at 100–150 mm. Coiling is evolute, with a moderately deep umbilicus which comprises 32–38% the diameter. The umbilical wall is rounded and undercut; the whorl section quadrate, with parallel sides, flattened shoulders, and a broad flattened venter. The greatest breadth is at the lateral tubercle and the whorl breadth to height ratio varies between 0·9 and 1·0. Ornament consists of 35–43 narrow, distant, rather delicate ribs per whorl. These arise at the umbilical seam and are low swellings across the umbilical wall. They usually strengthen at the shoulder into weak bullae and become wider and higher on the outer flank, which they cross in a rectiradiate to gently prorsiradiate direction. There is some variation in strength; in robust forms the ribs are straight, whereas in slender individuals they may be flexed. Most of the ribs are long and arise singly from bullae, but in some specimens they are untuberculate, passing the umbilical shoulder as mere striae, or rarely springing in pairs from a bulla. Occasional shorter, intercalated ribs, arising low or high on the flank, are also present. There are nine rows of tubercles; weak umbilical bullae; bullate laterals; stronger, conical inner ventrolaterals; strong feebly clavate or bullate outer ventrolaterals; and a weak siphonal set. On the venter the ribs commonly weaken between the outer ventrolateral and siphonal rows.

On bodychambers the ribs become markedly convex towards the adult aperture, the lateral and inner ventrolateral tubercles may weaken markedly, but the outer ventrolateral rows survive undiminished.

The sutures are poorly exposed in all our specimens but include a deep E, broad bifid E/L, narrow L, and relatively large, bifid L/U_2.

Discussion. Zázvorka's figures are side views only but show a densely and finely ribbed form which matches closely the Touraine material before us, as confirmed by casts of the holotype (text-fig. 6) and a Czech topotype (Pl. 45, figs. 3–4). These in turn are closely comparable with the poorly preserved holotype of *R.* (*R.*) *hispanicum* Wiedmann (= *R.* (*Proromaniceras*) *pseudodeverianum hispanicum* of Wiedmann 1960, 1964), which we take to be a synonym (Pl. 45, figs. 5–7). What appears to be the early developmental stages of this species are represented by a beautiful specimen from the Mancos Shale at USGS Mesozoic Locality 15925, in the southern part of the San Juan Basin, New Mexico (Pl. 45, fig. 2). At 17·5-mm diameter it shows a typical *Tunesites*-like stage, with deep, narrow, convex prorsiradiate constrictions flanked by narrow, rounded ribs bearing umbilical, ventrolateral, and siphonal tubercles, preceding a densely ribbed rectangular-whorled stage with nine rows of tubercles. The early development of *R. kallesi* is thus similar to that of *R. deverianum* (so far as this is visible in our specimens—cf. Pl. 39, figs. 7–10). In middle and later growth the two can be distinguished on the following criteria: *R. kallesi* is a small species; at a comparable degree of inflation it is delicately and narrowly ribbed; it has ribs that are dominant over weaker tuberculation; on the venter the ribs are narrower and more widely spaced and there is a tendency for the venter and flanks to remain flattened rather than becoming convex. It never develops the strongly clavate ventral and siphonal nodes of compressed (*uchauxiense*) individuals.

Two Touraine specimens, best referred to as *R.* aff. *kallesi*, show interesting features which point, even in this, the earliest species, to the origins of *R.* (*Yubariceras*) and *R.* (*Obiraceras*). AM 46 (Pl. 47, figs. 1–2), labelled '*Acanthoceras ornatissimum* Stoliczka, Saumoussay (M et L), Collection Valontaire', is a mature specimen with the following dimensions: D = 115·0(100); Wb = 50·0(43); Wh = 45·0(39); U = 36·5(32); Wb:Wh = 1·11; R = 36. It is septate to a diameter of approximately 70 mm, and on this portion the ribs are of unequal strength and length, those arising at the umbilicus

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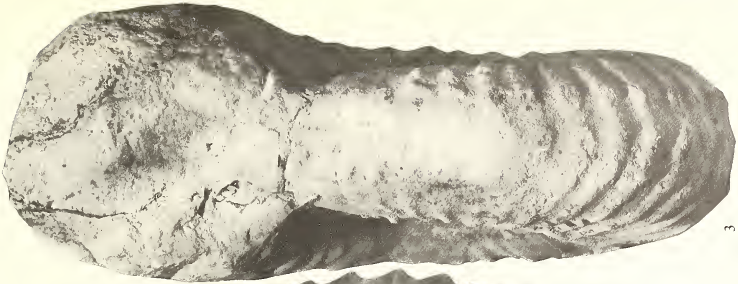
EXPLANATION OF PLATE 44

Figs. 1–3. *R.* (*Romaniceras*) *kallesi* Zázvorka. Adult specimen from Touraine in collections of the Museum d'Histoire Naturelle, Nantes.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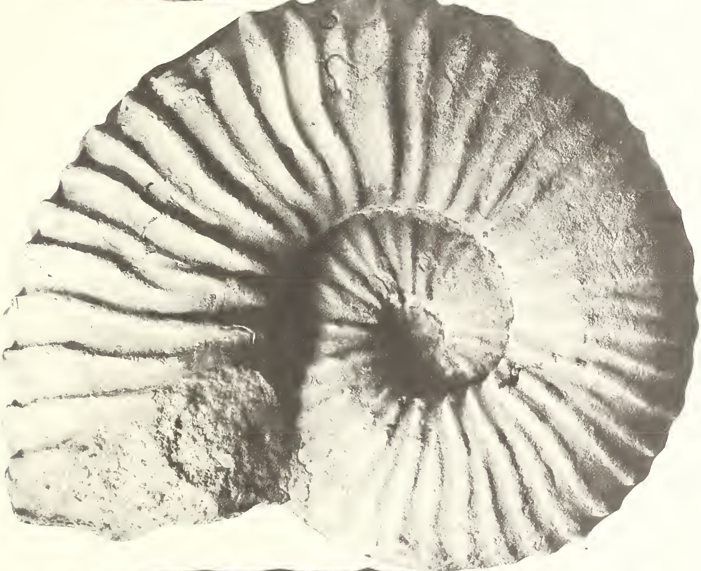
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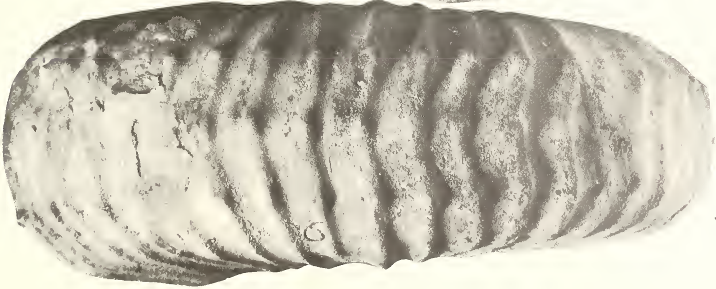
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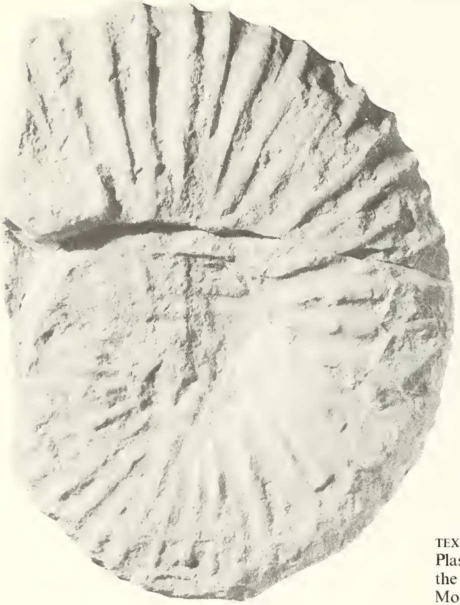
KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

having relatively strong bullae. All ribs bear weak inner and stronger outer lateral bullae, together with strong inner and outer ventrolateral and siphonal tubercles. On the body chamber the outer lateral tubercles have disappeared and the inner lateral are weak, leaving a total of only nine rows, while there are many more intercalated ribs. The over-all style and proportions link this specimen to *R. kallesi* but the eleven rows of tubercles of the phragmocone suggest affinities with *R.* (*Yubariceras*); we would suggest that this may indeed be an intermediate in which *R.* (*Yubariceras*) features are developed only briefly and not retained to maturity.

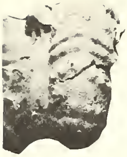


TEXT-FIG. 6. *R.* (*Romaniceras*) *kallesi* Zázvorka. Plaster cast of the holotype, no. 36938, from the Turonian Spongolith facies of the White Mountain, near Prague.

EXPLANATION OF PLATE 45

Fig. 1. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). Ventral view of an unregistered MNHP specimen (de Grossouvre collection), showing constrictions.

Figs. 2–7. *R.* (*Romaniceras*) *kallesi* (Zázvorka). 2 is a cast of a specimen from the Mancos Shale, *Prionocyclus hyatti* Zone, at USGS Mesozoic Locality 15925, San Juan Basin, New Mexico. The original is in the U.S. Geological Survey Collections, Denver. 3–4 are of BMNH 88992, a cast of a specimen from the Weisserberg, Czechoslovakia. 5–7 are of casts of the holotype of *Romaniceras* (*Proromaniceras*) *hispanicum* Wiedmann, the original is from an unknown horizon near Cidad, Burgos, Spain, and is in the Ciry collection, housed in the Institut de Géologie, Université Dijon.



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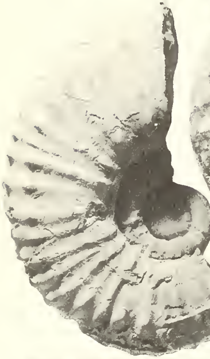

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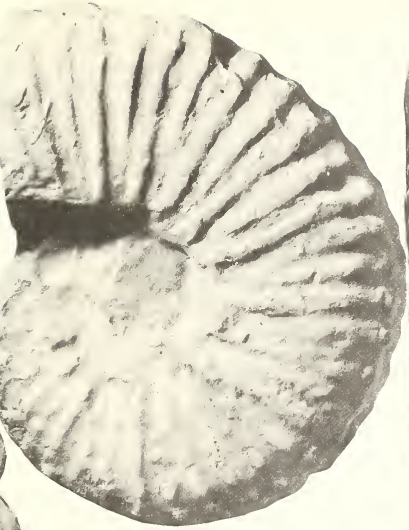

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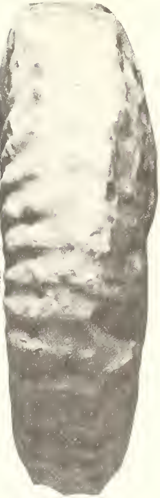

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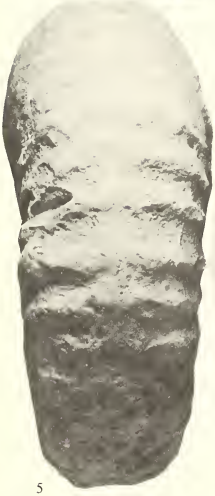

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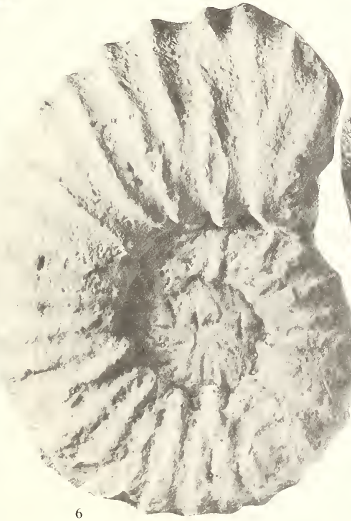

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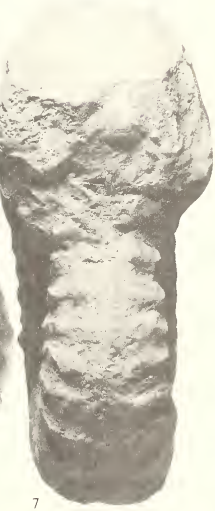


7

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

The second specimen, AM 33 (Pl. 47, figs. 3–4), also labelled '*Acanthoceras ornatissimum* Stoliczka', is from Montsoreau (Maine et Loire). Although clearly of the *kallesi* group, it shows an incipient doubling of the outer ventrolateral tubercles (more readily felt than photographed—Pl. 47, fig. 3), suggesting affinity with *R.* (*Obiraceras*) in which both inner and outer ventrolateral tubercles have this feature.

Occurrence. Early mid Turonian of western Czechoslovakia; Touraine, France; Burgos, Spain; and possibly New Mexico, U.S.A.

Subgenus *Yubariceras* Matsumoto, Saito, and Fukada, 1957
Romaniceras (*Yubariceras*) *ornatissimum* (Stoliczka)

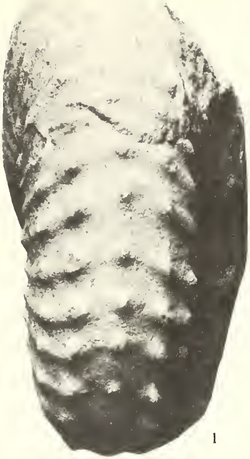
Pl. 39, figs. 1–6; Pl. 40, figs. 1, 3–5; Pl. 45, fig. 1; Pl. 48, figs. 1–4; Pl. 49, figs. 1–8; Pl. 50, figs. 1–4; text-figs. 3E, 7, 8

1863 *Ammonites deverianus* d'Orbigny; Pictet, p. 36, pl. 7.
1865 *Ammonites ornatissimus* Stoliczka, p. 75, pl. 40.
1889 *Ammonites deverioides* de Grossouvre, p. 524, pl. 12, figs. 1, 2 (including varieties *inermis* and *armata*).
1896 *Ammonites deverioides* de Grossouvre; Peron, p. 21, pl. 1, figs. 2–3.
1897 *Acanthoceras ornatissimum* Stoliczka; Kossmat, p. 16.
1901 *Acanthoceras Bizeti* de Grossouvre, p. 780.
?1924 *Acanthoceras Shastense* Reagan, p. 242, pl. 20, figs. 1, 2; pl. 60, fig. 5.
1931 *Romaniceras cumminsi* Adkins, p. 43, pl. 3, fig. 6.
1931 *Romaniceras loboense* Adkins, p. 44, pl. 2, figs. 1, 21; pl. 3, fig. 5.
1937 *Acanthoceras deverianum* d'Orbigny; Basse, p. 180, pl. 8, figs. 1*a–h*, 2*a–b*.
1939 *Romaniceras deverioïdes* de Grossouvre; Collignon, pp. 90 et seq.
1939 *Romaniceras ornatissimum* Stoliczka; Collignon, pp. 90 et seq.
1947 *Acanthoceras ornatissimum* Stoliczka; Lecointre, pl. 2, fig. 6.
non 1955 *Romaniceras* aff. *deverioide* (de Grossouvre); Reyment, p. 46, pl. 9, fig. 1*a–b*; text-figs. 18*b*, 19.
1957 *Yubariceras yubarense* (ex Yabe MS.) Matsumoto, Saito and Fukada, p. 27, pl. 8, fig. 1; pl. 10, fig. 1; pl. 11, fig. 1; pl. 13, fig. 1; pl. 15, fig. 1; text-figs. 8–9.
?1958 *Acanthoceras shastense* Reagan; Anderson, p. 242, pl. 20, figs. 1–2; pl. 60, fig. 5.
1958 *Mantelliceras conquistador* Anderson, p. 245, pl. 15, fig. 2.
1958 *Romaniceras hesperium* Anderson, p. 246, pl. 23, fig. 1, 1*a*.
?1959 *Eucalycoceras* (?) *shastense* (Reagan); Matsumoto, p. 94, pl. 23, fig. 1*a–c*; pl. 24, figs. 2*a–b*, 3*a–b*; text-figs. 47–49.
1959 *Romaniceras deverioide* (de Grossouvre); Matsumoto, p. 87, pl. 25, fig. 1*a–c*; pl. 26, fig. 1*a–c*; pl. 28, fig. 1*a–b*; pl. 29, fig. 4*a–c*; text-figs. 40–44.
1965 *Yubariceras yubarense* Matsumoto; Collignon, p. 24, pl. 385, fig. 1657.
1969 *Romaniceras deverioide* (de Grossouvre); Freund and Raab, p. 7.
1975 *Romaniceras deverioide* (de Grossouvre); Matsumoto, p. 121, pl. 15, fig. 2*a–b*; text-fig. 7.
?1975 *Romaniceras* [New Genus?] *aequicostatum* Matsumoto, p. 124, pl. 15, fig. 3*a–b*; text-fig. 8.
1975 *Yubariceras yubarense* Matsumoto, Saito and Fukada; Matsumoto, p. 133, pl. 19, fig. 1*a–b*; text-fig. 11.
1975 *Yubariceras* sp. aff. *Y. ornatissimum* (Stoliczka); Matsumoto, p. 135, pl. 17, fig. 2; pl. 18, fig. 1.
1975 *Yubariceras ornatissimum* (Stoliczka); Matsumoto, text-fig. 12.

EXPLANATION OF PLATE 46

Figs. 1–4. *R.* (*Romaniceras*) *kallesi* (Zázvorka). 1–2, AM 47, from Saumoussay, Maine-et-Loire. 3–4, AM 45, from Saumur, Maine-et-Loire.

PLATE 46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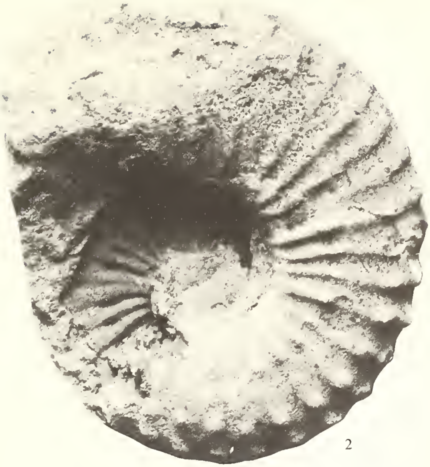
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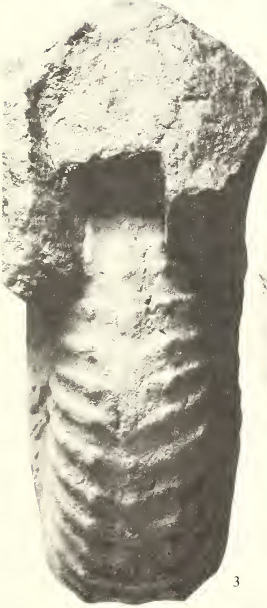
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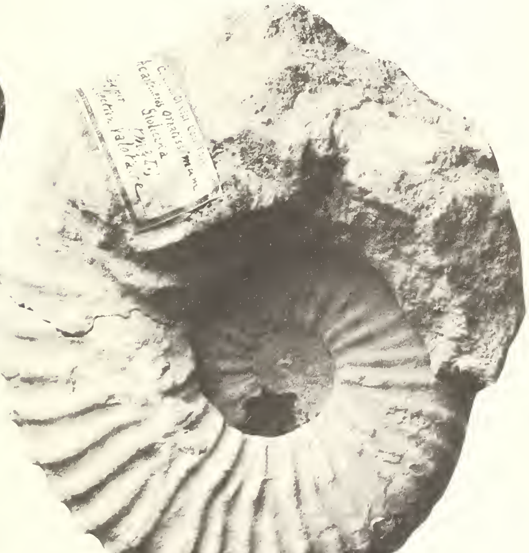
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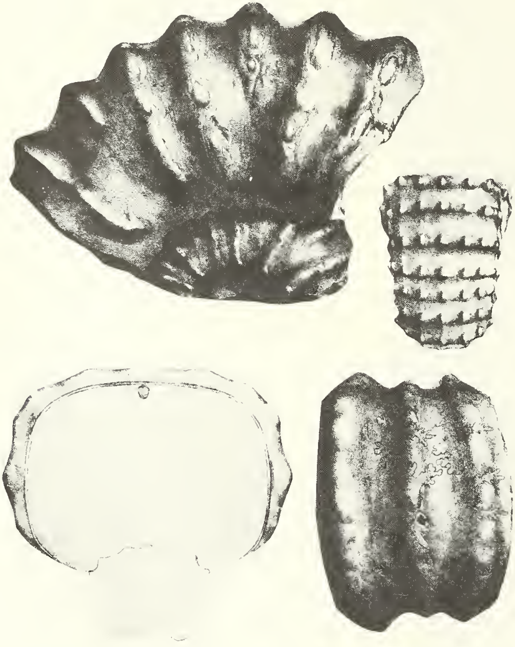
KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Type. The holotype, by monotypy, is the original of Stoliczka's (1865), p. 75, pl. 40, fig. 1*a–e*. This specimen is preserved in the collections of the Indian Geological Survey at Calcutta, no. 174, and is from the Uttatur Group at Odium, southern India (see text-fig. 7).

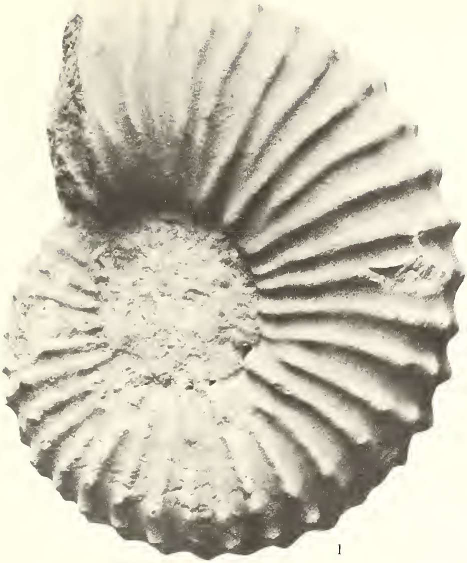
Other material studied. We have seen over thirty specimens, mostly from either Bourré (Loire-et-Cher) or Poncé (Sarthe), and there is material in most of the large French and British collections. From Bourré: the lectotype of *R. deverioides* (= de Grossouvre 1889, pl. 12, figs. 1–2) in the collections of the Ecole des Mines; MNHP 1896-27, de Vibraye collection; MNHP (unregistered) a 50-mm nucleus and part of a strongly tuberculate outer whorl. Numerous unregistered specimens: EMP, MNHP, SP, FSM, FSR. BMNH 34593, 37689, and C74804: FSM 13.962.



TEXT-FIG. 7. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka); copy of Stoliczka's (1865). Figures of the holotype. Reduced ×0·5 approx.

EXPLANATION OF PLATE 47

Figs. 1–4. *R.* (*Romaniceras*) aff. *kallesi* (Zázvorka). 1–2, AM 46, from Saumoussay, Maine-et-Loire, with eleven rows of tubercles on the phragmocone, suggesting affinities with *R.* (*Yubariceras*). 3–4, AM 33, from Montsoreau, Maine-et-Loire, with incipient doubling of outer ventrolateral tubercles, suggesting affinities with *R.* (*Obiraceras*).



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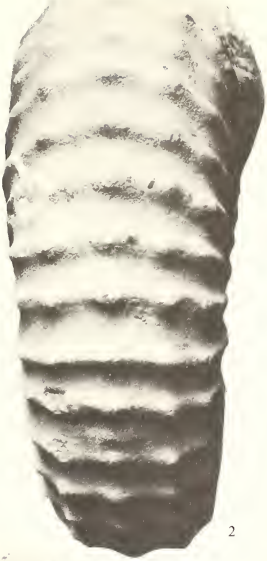

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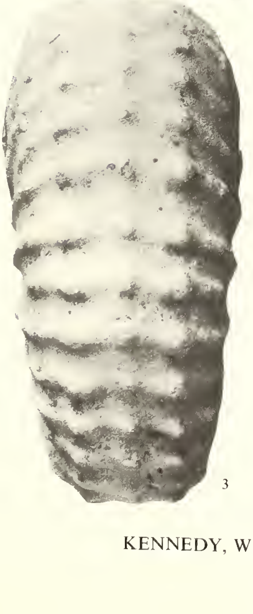

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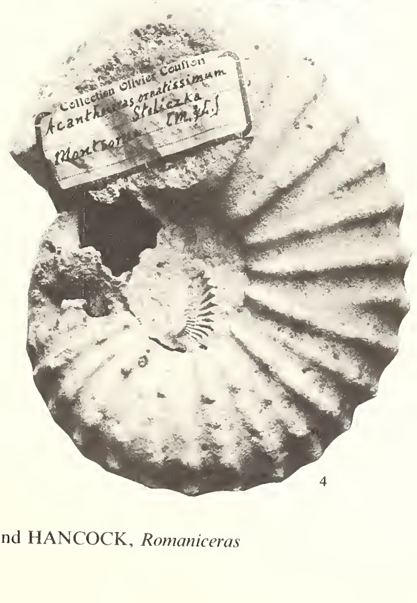
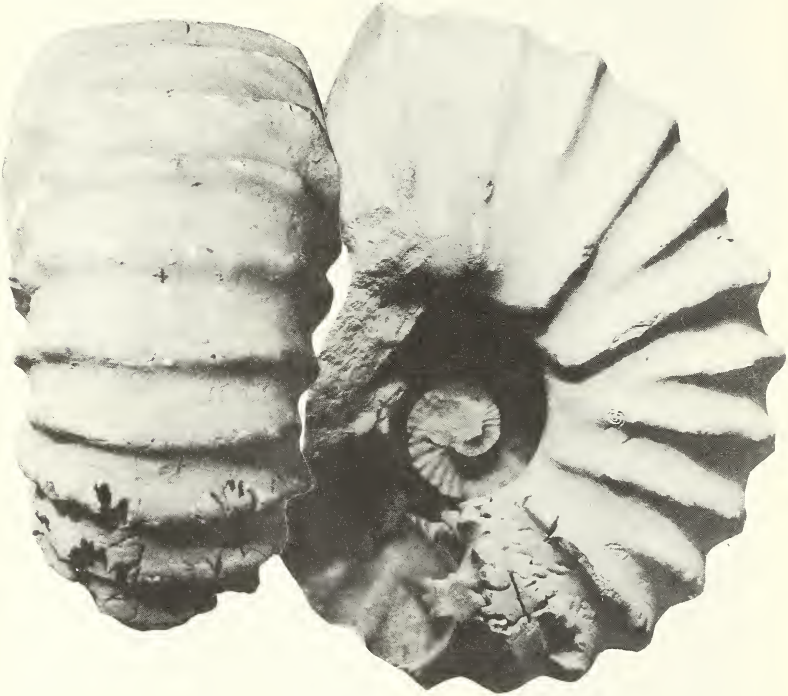


4

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

From Poncé: EMP A301, 'Collection Laville, June 15, 1897'; MNHP 6781a (d'Orbigny collection), four individuals, including that figured by Basse (1937, pl. 8, fig. 2*a–b*) as a 'co-type' of *R. deverianum*; MNHP, 3 unregistered specimens labelled 'Environs de Poncé, Rive dr. du Cher (Sarthe)' and 'Carrières de Ruille'; MNHP 1896-27, 170 mm in diameter; MNHP unregistered, a 165-mm long fragment. MNHP 1895-9, collection Durand; MNHP unregistered, but labelled '*R. ornatissimum*, Ligerian sup. Poncé, Sarthe'. BMNH C2798; FSL 13. 96.3. Numerous unregistered specimens: EMP, MNHP, SP, FSM, FSR.

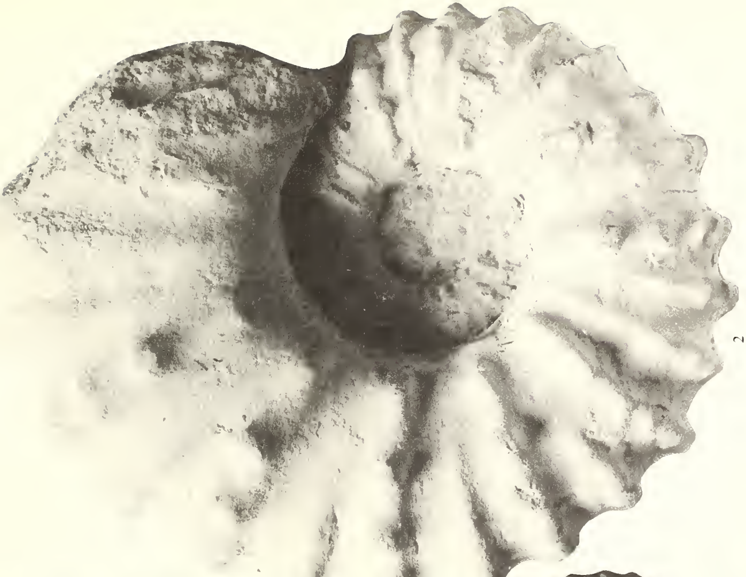
From Montrichard (Loir et Cher) MNHP 6781b (d'Orbigny collection). From Tourtenay (Deux Sevres): FSL 13966 'Touraine'; MNHP 6781c (d'Orbigny collection).



TEXT-FIG. 8. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). Adult bodychamber in the collections of the Faculté des Sciences, Le Mans, from Poncé, Sarthe. Reduced ×0·45.

EXPLANATION OF PLATE 48

Figs. 1–4. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). 1–2, the lectotype of *Ammonites deverioides* de Grossouvre, from Bourré, Loir-et-Cher. 3–4, MNHP 6781a (d'Orbigny collection) from Poncé, Sarthe, figured by Basse (1937, pl. 8, fig. 2*a–b*) as a 'co-type' of *Romaniceras deverianum*.



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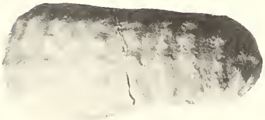

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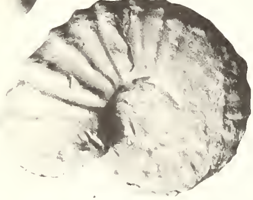

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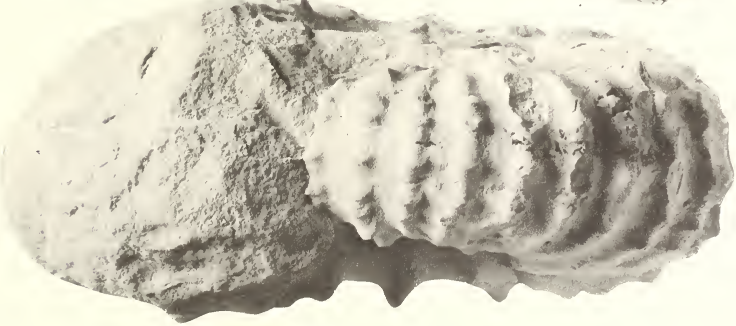


1

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Extra-European specimens include the following: OUMKT 993–996 (ex W. Popenoe collection) from the Bed of Swede Creek, in the Redding area of Shasta County, California; the types of *R. cumminsi* Adkins and *R. loboense* Adkins (Memorial Museum, Austin, Texas); and the types and other specimens of the following Japanese species (details in Matsumoto 1975): *Y. yubarense* Matsumoto, Saito and Fukada, *R. deverioide* of Matsumoto 1975; *R. aequicostatum* Matsumoto and *Yubariceras* aff. *Y. ornatissimum* Stoliczka.

Dimensions

	D	*Wb*	*Wh*	*Wb:Wh*	*U*	*Ribs*
Lectotype of *R. deverioide*	122·5(100)	62·0(51)	51·8(42)	1·19	38·3(31)	26/27
EMP;	at 98·2(100)	52·5(53)	43·0(44)	1·22	30·0(31)	26/27
MNHP 6781b (D'Orbigny coll.)	at 100 (100)	47·0(47)	41·0(41)	1·15	31·8(31·8)	27/28
MNHP 1896-27 (coll. Vibraye)	135·0(100)	61·6(46)	55·0(41)	1·12	44·5(33)	—
MNHP 6781 (d'Orbigny coll.)	150·0(100)	61·5(41)	57·0(38)	1·1	53·5(36)	32/33
MNHP 6781a (d'Orbigny coll.)	51·7(100)	22·7(44)	21·1(41)	1·1	— (—)	—
MNHP unregistered	a 73·5(100)	40·3(55)	32·5(44)	1·24	— (—)	24/25
Poncé, Carr. de Ruillé	at b 61·0(100)	31·7(52)	26·4(43)	1·2	— (—)	—
MNHP 6781a (coll. d'Orb.)	at 120·0(100)	51·5(43)	37·5(31)	1·37	— (—)	30/31
MNHP 1896-27	at 143·0(100)	78·0(55)	63·5(44)	1·23	43·2(30)	26
MNHP	c 145·0(100)	90·0(62)	62·0(43)	1·45	45·8(32)	25/26
Liger Sup.	ic 145·0(100)	76·0(52)	57·0(39)	1·33	45·8(32)	25/26
Poncé	c 120·0(100)	68·0(57)	53·0(44)	1·28	38·0(32)	26/27

Description. The smallest individual we have seen is a nucleus extracted from a Californian example kindly sent by Professor W. Popenoe; illustrated as Pl. 39, figs. 1–6, it shows a typically constricted '*Tunesites*' nucleus; this can also be seen in our photograph (Pl. 40, fig. 1) of the specimen GK.H5685 figured by Matsumoto (1975, pl. 15, fig. 2*a*–*b*). These link with the smallest Touraine specimens, illustrated as Pl. 45, fig. 1, Pl. 48, figs. 3–4, and Pl. 49, figs. 1–4, which vary from rather slender to depressed individuals, which are evolute, with an umbilicus of moderate depth and a rounded to reniform intercostal section with a broadly rounded venter.

There is great variation in rib density, from 25 to 35 per whorl. In some individuals the ribs are straight and recti- to prorsiradiate, mostly extending to the umbilicus with weak to strong umbilical bullae (Pl. 49, figs. 1–2). There may be branching of ribs from bullae (Pl. 49, figs. 3–4), whilst intercalated ribs are very variably developed, sometimes arising low on the flank (Pl. 49, fig. 3), sometimes not starting until just below the shoulder. There are a total of eleven rows of tubercles: umbilical, lateral, inner and outer ventrolateral, ventral, and siphonal.

Umbilical tubercles are commonly bullate; laterals vary from bullate to rounded/conical, the remainder may be rounded to clavate. There is wide variation in relative strength and spacing of tubercles, although the lateral tubercle is often strong. Constrictions are prominent but sparse (up to 5?) on all juveniles, occurring up to 50 mm diameter. They parallel the ribs and are most strongly developed across the venter.

In middle and later growth, it is convenient to describe the specimens under three groups:

Form A (= R. deverioides *de Grossouvre*) (*Pl. 48, figs. 1–2; Pl. 49, fig. 8*)

The whorl section is depressed, with a whorl breadth to height ratio of around 1·2, with a relatively low whorl expansion rate. Ribs alternate regularly long and short, the long ribs bearing a full complement of eleven rows of tubercles; short ribs bear only seven.

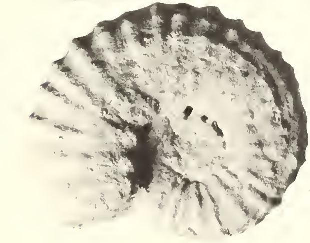
Form B (*typical* ornatissimum) (*Pl. 50, figs. 3–4*)

An inflated form, with very broad, flattened venter and a reniform, very depressed whorl section. The lateral tubercle tends to be lengthened into a spine in some individuals.

Forms A and B reach a massive size (up to 500 mm) and are connected by gradations at all sizes.

EXPLANATION OF PLATE 49

Figs. 1–8. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). 1–2, MNHP 6581 (d'Orbigny collection), Poncé, Sarthe. 3–4, MNHP, de Grossouvre collection, Poncé, Sarthe. 5–7 is a square-whorled specimen from Touraine close to the holotype of *Yubariceras yubarense* illustrated in Plate 40, figs. 3–5. 8, ventral view of the lectotype of *Ammonites deverioides*; see explanation of Plate 48 for details.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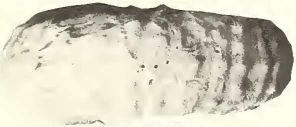
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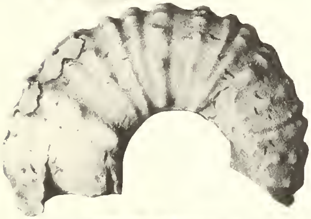
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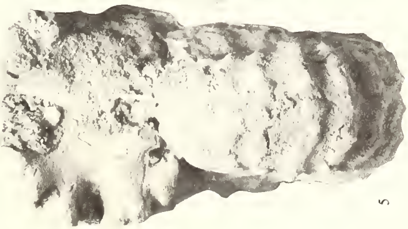
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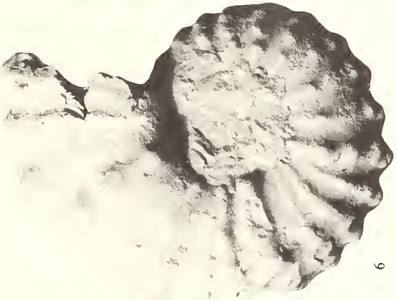
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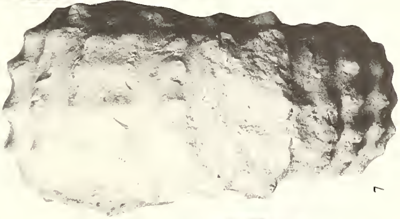
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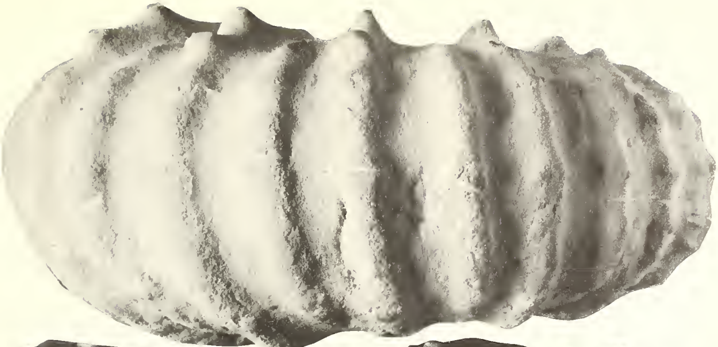
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KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Form C (inerme *de Grossouvre*) (*Pl. 50, figs. 1–2*)

A slender, slowly expanding form; tubercles are subsidiary to ribs and may disappear altogether at diameters of 100 mm upwards. Juveniles are connected by gradations to Form B above; adults are distinct.

We believe that A and B are probably macroconchs and C are microconchs.

The suture line (text-fig. 3E) is of basic *Acanthoceras* type, with broad bifid saddles and narrower lobes.

Discussion. The Touraine populations of *R.* (*Y.*) *ornatissimum* show very wide variation, although all pass through smooth serpenticone constricted ribbed and multituberculate stages during early growth. In middle growth there is great variation in inflation and relative strength of tubercles and ribs, as well as relative development and spacing of tubercles. Onset of adult features—chiefly loss of tubercles and dominance of ribs—occurs at disparate sizes; we have some individuals adult at 120 mm and others which approach 500 mm. These suggest that there may be an as yet unconfirmed dimorphism in the group, although it must be admitted that most specimens are either large phragmocones or adults and that small adults are rare.

This range of variation is not unusual in acanthoceratids (e.g. Kennedy and Hancock 1970; Juignet and Kennedy 1977) and we are confident that but a single species is present, as is shown by the continuous variation in our series. De Grossouvre (1889) was well aware of this variation and used three names for his material, *deverioides* and vars. *inermis* (renamed *Acanthoceras bizeti* in 1901, p. 780) and *armata*.

Although a lectotype of *R. deverioides* has been designated (Matsumoto 1959, p. 87), there are no specimens which can be proved to be those which de Grossouvre had in mind when creating his varieties. It is, however, clear that he studied the many *Romaniceras* from localities such as Loches, Bourré and Poncé, including those in the École des Mines, Muséum d'Histoire Naturelle and Sorbonne, amongst other museums. In order to provide an objective basis for discussion we would therefore designate as lectotype of *Acanthoceras deverioides inerme* the fine specimen in the School of Mines illustrated as Pl. 50, figs. 1–2, EMP A301, Laville coll., from Poncé. As lectotype of *A. deverioides armatum*, we designate the Poncé specimen in the Muséum d'Histoire Naturelle illustrated as Pl. 50, figs. 3–4.

Subsequent interpretations of *R. deverioides* have varied greatly, but there have been two main schools. Kossmat, the first revising author, concluded that *R.* (*Y.*) *deverioides* was a strict synonym of *R.* (*Y.*) *ornatissimum* (Stoliczka) (Kossmat 1898, p. 132, text-figs. 2–4) on the basis of the comparable whorl section of Stoliczka's type and a specimen from Ruillé (Sarthe). This view was also taken by Diener (1925) and Zázvorka (1958).

In contrast, Collignon (1939, p. 37) retained *deverioides* and *ornatissimum* as separate species on the grounds that in the former the whorl section is higher than wide, the ribs are straight, and the tubercles are sharp instead of round and blunt. Perhaps the clearest statement on the forms of *R.* (*Y.*) *deverioides* comes from Matsumoto (1959) who thought *R. deverioides* specifically distinct from *R. ornatissimum*, of which he regarded *R. deverioides armatum* a synonym, with *R. inerme* as a further separate species.

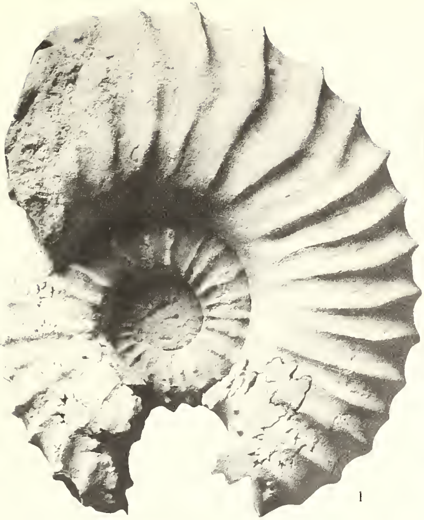
In 1975 Matsumoto placed *deverioides* and *ornatissimum* in different genera, referring the former to *Romaniceras* and the latter to *Yubariceras*.

The Sarthe populations before us include medium-sized individuals, in particular those which have been referred to as *R.* (*Y.*) *deverioides armatum*, which match in all respects the holotype of *ornatissimum*. Furthermore, these intergrade with *R.* (*Y.*) *deverioides deverioides* and we see no basis for separating these forms. *R. deverioides inerme* is also no more than a variant or perhaps dimorph. We retain none of these as separate species.

EXPLANATION OF PLATE 50

Figs. 1–2. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). Lectotype of *Ammonites deverioides* var. *inermis* de Grossouvre, EMP A301, Laville Collection, Poncé, Sarthe. Reduced ×0·6 approximately.

Figs. 3–4. *R.* (*Yubariceras*) *ornatissimum* (Stoliczka). MNHP 1826–27, from Poncé, Sarthe, the lectotype of *Ammonites deverioides armatum* de Grossouvre. Reduced ×0·6 approximately.



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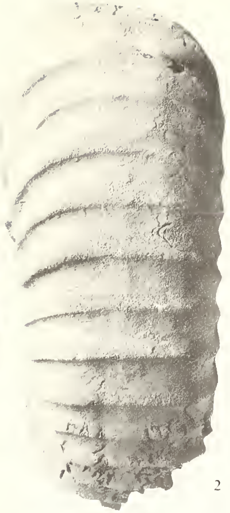

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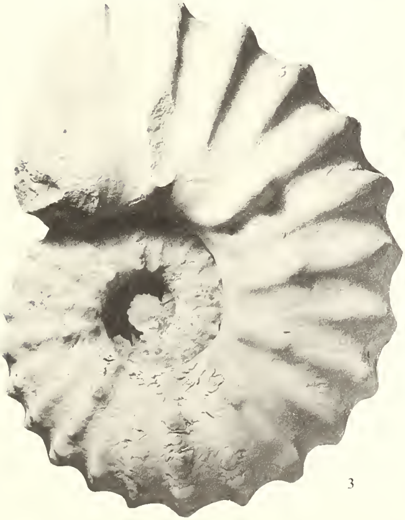
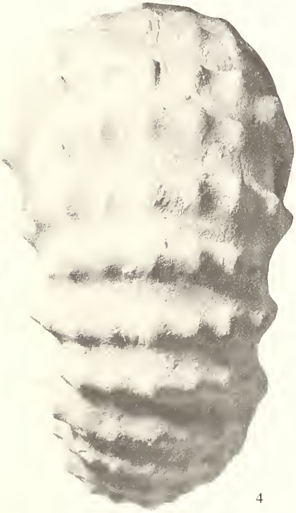


3



4

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Yubariceras yubarense (Matsumoto, Saito and Fukada) (1957, p. 27, pl. 8, fig 1; pl. 10, fig. 1; pl. 11, fig. 1; pl. 13, fig. 1; pl. 15, fig. 1; text-figs. 8–9; Matsumoto 1975, p. 133, pl. 19, fig. 1; text-fig. 11) is based on a series of specimens from Hokkaido; the holotype is refigured here as Pl. 40, figs. 3–5). Matsumoto (1975, p. 135) separated *R.* (*Y.*) *yubarense* from *R.* (*Y.*) *deverioides* in that the former had a square-whorled, *Acanthoceras*-like shell form and the latter a round-whorled *Calycoceras*-like shell form, and that constrictions extended to middle growth in *Y. yubarense* and were in general better marked. As can be seen from Pl. 45, fig. 1, the constrictions of the Touraine material are as strong as those of the Japanese, whilst several Touraine specimens have similarly quadrate whorls (e.g. Pl. 49, figs. 5–7). Matsumoto (1975, p. 135) distinguished *Y. yubarense* from *Y. ornatissimum* in that the ribs of the former were weaker, and inner lateral tubercles not so distinct. Again, these are differences between individuals only. So far as can be seen the only specific criterion remaining is the quadrate whorl of *Y. yubarense*, which occurs in some of the European *R. ornatissimum*. The juvenile figured by Matsumoto (1975, pl. 19, fig. 1) is relatively round whorled, so that even this distinction may not be invariate. We do not, therefore, consider that *Y. yubarense* can be maintained as either a separate species or subspecies, although it is possible that the mean of the Japanese population may differ somewhat from that of Touraine.

R. aequicostatum Matsumoto (1975, p. 124, pl. 15, fig. 3, text-fig. 8) is based on a unique specimen from the Turonian of a tributary of the Ikushumbets, Hokkaido; its precise horizon is unknown. It was characterized by (1) small size (68 mm), (2) depressed whorl (–wb : wh ratio is 1·4–1·5), (3) distant strong, long ribs without intercalatories, and (4) eleven rows of tubercles, the ventral three clavate, ventrolaterals sharply pointed, upper laterals smaller, lower laterals prominent, and umbilicals small but distinct (Matsumoto 1975, p. 124).

The holotype is in fact badly deformed and incompletely visible; it can be matched in our Touraine juveniles in many respects, except for its greater depression and absence of secondary ribs. Whorl section may be of no more than intraspecific significance and certain larger specimens have very depressed whorls, whilst some Touraine specimens (e.g. Pl. 48, fig. 4) have predominantly, but not exclusively, long ribs. In the absence of better material we can only take the view that it is probably a juvenile *R. ornatissimum*.

R. (*Y.*) *kanei* Jones (1938, p. 120, pl. 8, figs. 2, 7, 8; pl. 9, fig. 6; see also Matsumoto 1975, p. 123, pl. 19, fig. 4) is based on a single specimen from an unknown locality and horizon in Coahuila, Mexico, refigured here as text-fig. 9. It is readily separable from *R. ornatissimum* by its evolute, almost serpenticone, coiling and slowly expanding, polygonal whorl section.

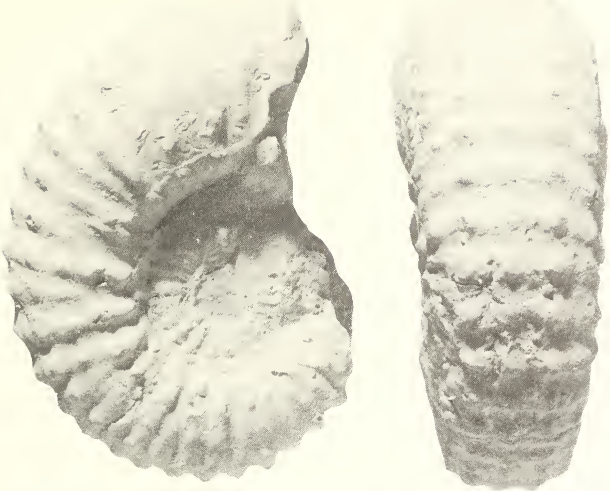
The *Romaniceras* from Texas described by Adkins (1931) are both synonyms of *R. ornatissimum*; *R.* (*Y.*) *loboense* Adkins (1931, p. 44, pl. 2, figs. 1, 21; pl. 3, fig. 5), is based on a poorly figured fragment; the holotype of *R.* (*Y.*) *cumminsi* Adkins (1931, p. 43, pl. 3, fig. 6) is an adult 330 mm in diameter.

Mantelliceras conquistador Anderson (1958, p. 245, pl. 15, fig. 2), *M.* aff. *conquistador* Anderson (1958, p. 245, pl. 14, fig. 2) and *R. hesperium* Anderson (1958, p. 246, pl. 23, fig. 1, 1*a*) are further synonyms based on Californian material, and are discussed by Matsumoto (1958, pp. 87–92).

Acanthoceras shastense Reagan (1924, p. 179, pl. 18, fig. 1; see Matsumoto 1959, p. 94, pl. 23, fig. 1*a*–*c*; pl. 24, figs. 2*a*–*b*, 3*a*–*b*; text-figs. 47–50) is a *R.* (*Yubariceras*) which occurs in the same member as *R.* (*Y.*) *ornatissimum* in California. It can be matched in the variants of *R.* (*Y.*) *ornatissimum* from Touraine which mature at a relatively small size and show an early decline of tubercles (e.g. de Grossouvre's *inermis*); as with the Touraine occurrence it is tempting to regard these as the microconch of the species.

The *Romaniceras* aff. *deverioides* of Reyment (1955, p. 46, pl. 9, fig. 1*a*–*b*) has nine rows of tubercles and the outer ventrolateral shows distinctive doubling, suggesting the specimen is an *Obiraceras*.

Occurrence. *R.* (*Y.*) *ornatissimum* is a typically mid Turonian species known from southern England; Sarthe, Touraine, and Vaucluse in France; the Lebanon; Israel; Tunisia; Madagascar; southern India; Japan; Mexico; and California and Texas in the United States.



TEXT-FIG. 9. *R.* (*Yubariceras*) *kanei* (Jones). Plaster cast of the holotype (Jones 1938, p. 120, pl. 8, figs. 7–8), University of Michigan collections no. 16819, from an unknown locality and horizon in Coahuila, Mexico.

CONCLUSIONS

From our study of the development and variation in more than 150 specimens of *Romaniceras* that we have seen, we suggest that the following species be recognized:

R. (*Romaniceras*)

1. *R.* (*R.*) *deverianum* (d'Orbigny)
2. *R.* (*R.*) *kallesi* (Zázvorka)
3. *R.* (*R.*) *pseudomphalum* (Matsumoto)
4. *R.* (*R.*) *fujishimai* (Matsumoto)

R. (*Yubariceras*)

1. *R.* (*Y.*) *ornatissimum* (Stoliczka)
2. *R.* (*Y.*) *kanei* (Jones)
3. *R.* (*Y.*) *aequicostatum* Matsumoto

R. (*Obiraceras*)

1. *R.* (*O.*) *ornatum* (Matsumoto)
2. *R.* (*O.*) sp. (= *R.* aff. *deverioides* and *R. uchauxiense* of Reyment, 1955).

Phylogeny and stratigraphy

Romaniceras evolved from *Kamerunoceras* (Kennedy and Wright 1979). The earliest known *Kamerunoceras* itself is from high in the Cenomanian of Devon (Bayliss collection) and is morphologically intermediate between *Euomphaloceras septemseriatum* (Cragin) and *Kamerunoceras turoniense* (d'Orbigny) (= *K. salmuriense* (Courtiller)). *R.* (*Romaniceras*) *kallesi* is still similar to a *Kamerunoceras*, differing only in its nine rows of tubercles, of which those on the venter are even in strength, instead of irregular as in *Kamerunoceras*; nor is there ever any trace of a keel in *Romaniceras*. *R. kallesi* is found alongside *K. turoniense* in the St Cyr-en-Bourg Fossil Bed of Touraine, which yields a range of ammonites which together distinguish a *R. kallesi* assemblage-zone, probably equivalent to Zone 7 of Wiedmann (1960) in north Spain, somewhere in the middle of the Turonian stage (Hancock, Kennedy, and Wright 1977).

There is no stratigraphic evidence to support the statement of Cooper (1978, p. 104) that *R.* (*Yubariceras*) appeared in the 'Lower Turonian', nor that *Romaniceras* s.s. was derived from an early form of *R.* (*Yubariceras*). The few records of 'Lower' Turonian *Romaniceras* are the result of the lack of standardization in the use of 'Lower', 'Middle', and 'Upper'. Thus Zázvorka (1958) records *R. kallesi* from the 'Lower' Turonian near Prague, but from the same area he also records *R. ornatissimum* from the lower part of the 'Middle' Turonian, the same stratigraphic order as is found in Touraine. Wiedmann (1960) recorded '*R. hispanicum*' from the 'Lower' Turonian of northern Spain, but the exact horizon of the specimen was actually unknown. The *Yubariceras* recorded by Collignon (1965, p. 24) from the 'Turonien inférieur' of Antsarona in Madagascar was associated with typical mid Turonian ammonites according to the list in Besairie and Collignon (1972, p. 281).

There is a stratigraphic gap in Touraine between *R. kallesi* and *R. deverianum* that is occupied by *R.* (*Y.*) *ornatissimum*. At present it is impossible to say whether *R. deverianum* is derived from *Yubariceras*, or whether it arose from *R. kallesi* in another region and then migrated back to western Europe. The succession in Japan fails to illuminate this point, but it is possible that Dr. W. A. Cobban's work on the Western Interior of the U.S.A. will give the answer.

Following de Grossouvre (1901) it has generally been assumed that *R. deverianum* marked the top zone of the Turonian, but in Touraine there are many minor disconformities between the horizon of *R. deverianum* and the overlying Coniacian. In England the few known *R. deverianum* come from below the Chalk Rock (Zone of *Subprionocyclus neptuni*) (Hancock, Kennedy, and Wright 1977). Thus the three species of *Romaniceras* described here all occur over a quite limited range within the middle of the Turonian stage, equivalent to the broad *Collignoniceras woollgari* Zone of authors.

R. (*Y.*) *ornatissimum*, the commonest and most widespread species of the subgenus, is found in Touraine stratigraphically between *R. kallesi* and *R. deverianum*. The records of Matsumoto (1975) shows that in Japan it ranges much higher. *R.* (*Y.*) *otatumei* extends from somewhere in the mid Turonian as high as the Zone of *Reesidites minimus*, now generally regarded as the highest zone of the stage. *Obiraceras ornatum* Matsumoto is probably also younger than any European *Romaniceras*.

There are no known descendants of *Romaniceras*.

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THE SCOTTISH LOWER CARBONIFEROUS SHARK *ONYCHOSELACHE TRAQUAIRI*

by J. R. F. DICK *and* J. G. MAISEY

ABSTRACT. The discovery near Edinburgh of a second articulated specimen of a small Carboniferous hybodontiform shark has encouraged renewed anatomical study of the original Glencartholm specimen. This shark is not referable to *Tristychius arcuatus* Agassiz, 1837, as previous authors have suggested, but has recently been renamed *Onychoselache traquairi* Dick, 1978. *Onychoselache* has a tribasal pectoral fin similar to most hybodontiforms and neoselachians, not a dibasal fin as is often supposed. Furthermore, the structure of the head and tail are typically hybodontiform and, therefore, there is no justification for its subordinal separation from the hybodontids, as proposed by Moy-Thomas (1936).

IN 1888 Traquair briefly described the pectoral fin of a small shark from Glencartholm in Dumfriesshire, which he identified as *Tristychius arcuatus* Agassiz, 1837. He noted that the fin was remarkably modern in appearance compared with those of other known Palaeozoic sharks. Its basal cartilages were highly differentiated and very similar to those of Recent elasmobranchs. In fact, the fin appeared to have only two basal cartilages, a mesopterygium and a metapterygium, rather than the three typical of most Recent forms. He concluded that the propterygium was either very small or had fused to the mesopterygium. Traquair never published a full description of the specimen, which is now in the Royal Scottish Museum (RSM), Edinburgh. However, he appears to have had doubts about its similarity to *T. arcuatus*, and in 1903 referred it to *Tristychius minor* Portlock in a faunal list of the Glencartholm locality.

A more complete description of the specimen was given by Woodward (1924). He noted small '*Lophodus*'-like teeth and peculiar hooked denticles along the anterior margins of the pectoral fins, and also described its finspines. He accepted Traquair's (1888) identification as *T. arcuatus*, and concluded that sharks closely related to Mesozoic hybodonts were already present in the Lower Carboniferous.

The fish was redescribed by Moy-Thomas (1936), who prepared the posterior part of the specimen to expose the pelvic fins, anal fin, and base of the tail. He noted that the pectoral and caudal fins appeared to be more specialized than in hybodontids, and suggested that it should be included in a separate Suborder, Tristychii, of the Order Protoselachii (Moy-Thomas 1936, 1939).

Both Woodward (1924) and Moy-Thomas (1936) upheld Traquair's (1888) dibasal interpretation of the pectoral fin. However, one of us suggested recently that the mesopterygium was displaced and could be overlying and concealing the propterygium (Maisey 1975, fig. 2*b* inset). As in other sharks, the calcified cartilage elements are composed of a thin external layer of prismatic calcified cartilage surrounding a central core which, in life, was probably filled with non-calcified hyaline cartilage. A vertical section through a cartilage might, therefore, be expected to expose two layers of calcified cartilage. Where the mesopterygium of the Glencartholm specimen is damaged, however, it is possible to identify four layers of calcified cartilage, as if two cartilages were present. Confirmation of this possibility was provided when a new specimen of this fish was collected by Mr. S. P. Wood from the Wardie Shales near Edinburgh. This specimen (RSM 1974.23.14), studied by the other author (J. R. F. D.), shows quite clearly that three basal cartilages are present in each pectoral fin.

The Wardie specimen is slightly larger than the Glencartholm fish but there can be little doubt that the two are conspecific. Both have similar teeth and pectoral fins and both have the characteristic series of hook-like, anterior marginal pectoral denticles.

Unfortunately, other material collected by Mr. Wood from the Wardie Shales and elsewhere in the Scottish Oil Shale Group indicates that this fish cannot be *T. arcuatus* Agassiz. Its finspines are

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distinctly different from the holotype of *T. arcuatus* and, while they are similar to *T. minor*, the spine of the latter appears to be indistinguishable from immature spines of several contemporaneous shark species. Therefore, the Glencartholm specimen has recently been made the holotype of a new genus and species, *Onychoselache traquairi* (Dick 1978).

The reidentification of the Glencartholm fish, together with new information on the head and pectoral fins provided by the Wardie specimen, have encouraged us to produce a full redescription of *O. traquairi*. We have also been able to reconsider its relationships with other early sharks in the light of new data obtained from the study of *T. arcuatus sensu stricto* (Dick 1978).

Abbreviations used in text and text-figs. MC, Meckel's cartilage; MSP, mesopterygium; MTP, metapterygium; NCR, neurocranium; PAX, pectoral fin axis; PQ, palatoquadrate; PRP, propterygium; R, radials; SC, scapulocoracoid; apq, articular process of palatoquadrate; cor, coracoid region of scapulocoracoid; dent, denticles; dfm, diazonal nerve foramen; fm, foramen magnum; pop, postorbital process; scp, scapular region of scapulocoracoid.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order HYBODONTIFORMES incertae familiae
Genus ONYCHOSELACHE Dick, 1978

Type and only known species. O. traquairi Dick, 1978.

Revised diagnosis. Small (160–250 mm long) hybodontiform sharks having a series of about twelve or fourteen large, hook-like denticles along the anterior margin of each pectoral fin; similar denticles present on head, sometimes fused at their bases into multicuspid scales. Teeth low-crowned and tumid, with deep roots lacking a lingual torus. Finspines with three or four thin costae each side; the hindmost finspine more recurved and stouter than the anterior one.

Onychoselache traquairi Dick, 1978

Holotype. RSM 1885.54.1, from the Glencartholm Volcanic Beds, C_2/S_1 Zone, Viséan (Lower Carboniferous) on the banks of the River Esk, near Glencartholm, Dumfries District (Galloway and Dumfries Region), Scotland.

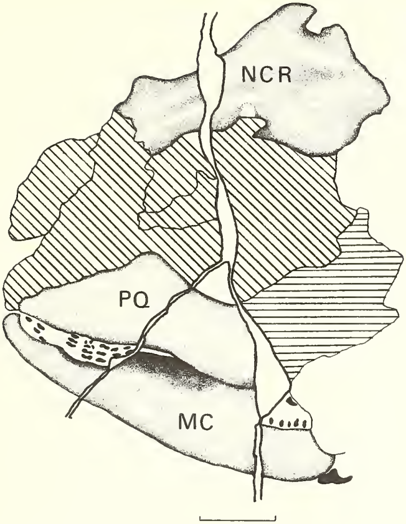
Referred material. RSM 1974.23.14A/B from nodule bed 7 (Wood 1975), Wardie Shales, C_2/S_1 Zone, Viséan, on the seashore between Granton Harbour and Trinity Bridge, Wardie, Edinburgh, Scotland.

Preservation. The Glencartholm specimen is preserved in a calcareous shale, while the Wardie specimen is in a clay-ironstone nodule. Because of the delicate state of both specimens, little additional preparation has been possible. The former is exposed in lateral view and is almost complete except for the tip of the tail. The latter specimen is exposed dorsoventrally, but extends only to the start of the pelvic region, to the base of the second dorsal finspine. The Wardie specimen is slightly the larger, suggesting a fish of about 250 mm total length compared with about 165 mm for the holotype.

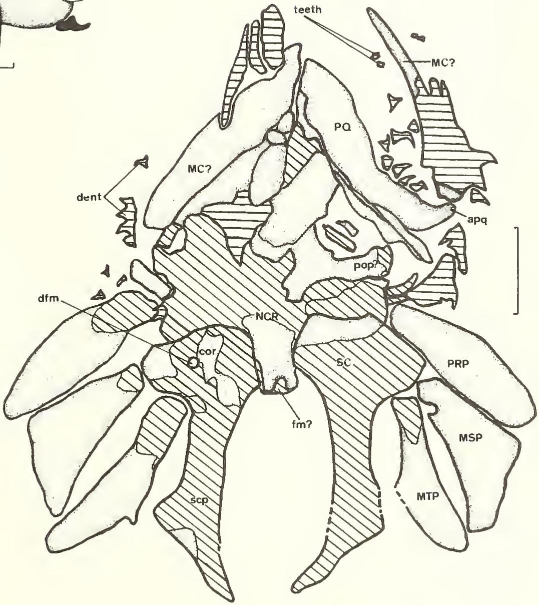
Description

Neurocranium and Jaws. The head of the holotype is badly crushed and has not previously been described. Like the trunk, it is exposed in lateral view, so that the left palatoquadrate, the right Meckel's cartilage, and parts of the roof and left side of the neurocranium can be identified (text-fig. 1). The neurocranium is about 24 mm long. The orbits lie almost midway along its length and are surmounted by marked supraorbital ridges.

The neurocranium of RSM 1974.23.14 is exposed in ventral view (text-fig. 2). Its occiput lies between the two coracoid parts of the pectoral girdle. The only feature of the neurocranium which can be distinguished further forward is a long process running laterally towards the left palatoquadrate. This is probably a postorbital process similar in structure to that of *T. arcuatus sensu stricto* (Dick 1978). Both specimens suggest that the otico-occipital region was proportionately as short as that of *Hybodus basanus* (Woodward 1916).



TEXT-FIG. 1. *Onychoselache traquairi*, RSM 1885.54.1. Braincase and jaws. Diagonal hatching is damaged cartilage. Horizontal hatching is an area of broken cartilage and denticles. Scale bar = 5 mm.



TEXT-FIG. 2. *Onychoselache*, RSM 1974.23.14A. Jaws, braincase, pectoral girdle, and pectoral basals. Scale bar = 10 mm.

The palatoquadrate of RSM 1885.54.1 is badly damaged posteriorly. Its anterior end is shallow and its jaw symphysis, which must have underlain the ethmoid region of the neurocranium, would have been narrow. A well-developed orbital process is present beneath the orbit on RSM 1885.54.1. The articular region of the left palatoquadrate is exposed on RSM 1974.23.14. The jaw is lying on its side, with the articular process for the lower jaw projecting laterally (text-fig. 2, apq). Although the otic process is incomplete, there is no suggestion of a long and deep quadrate region like that of most Palaeozoic sharks (Schaeffer 1967, 1975). The jaw may have been similar in shape to that of *T. arcuatus* (Dick 1978, fig. 10A–D) and probably terminated beneath the postorbital process of the neurocranium.

The right Meckel's cartilage is exposed in mesial aspect on the holotype. Part of a deep dental furrow for the tooth families can be seen beneath the orbital process of the palatoquadrate. The lower jaw deepens posteriorly, but its articular surface is obscured.

Branchial arches. Nothing is preserved of the branchial arches in RSM 1974.23.14, and very little can be identified in the holotype. However, Woodward (1924, fig. A, br) noted the presence of a few long, thin cartilages, lying horizontally along the body above the left scapulocoracoid, which he identified as branchial rays. He suggested that the pectoral girdle of the holotype was slightly displaced, but Moy-Thomas (1936, fig. 12) restored the coracoid region of the scapulocoracoid running beneath the branchial arches and almost extending forward to the back of the jaw. This results in an unnaturally high position for the branchial arches, whose ventral elements would still have lain well above the level of the jaw articulation.

We believe, for reasons explained below, that the left scapulocoracoid of the holotype has been displaced forward so that most of the branchial cartilages have been lost. Those cartilages identified by Woodward (1924) as branchial rays may in fact be the pharyngobranchial elements of the gill arches, displaced forwards and upwards by the scapulocoracoid until they came to lie in the horizontal plane. Alternatively, they may be hyoid rays similar to those of *T. arcuatus* (Dick 1978), but it is far more likely that both branchial and hyoid rays would be lost before the much stouter visceral arches to which they were attached.

Vertebral column. The axial skeleton of both specimens is similar, although the Wardie specimen's vertebral column is partly disarticulated. There are no vertebral centra and presumably the notochord was unconstricted. The neural arches, ribs, and haemal arches are calcified; the neural arches are stout, but the ribs are long and slender. Those of the Wardie specimen are apparently broken, and consequently appear shorter than in the holotype.

Dorsal fins. Moy-Thomas (1936, p. 776) noted the presence of a single, short radial cartilage behind the triangular basal of the second dorsal fin. While the poor preservation of this region makes interpretation difficult, there is probably at least one more radial and there may even have been a series of cartilages similar to those in *Hybodus hauffianus* (Woodward 1916, fig. 2).

The internal structure of the first dorsal fin of the Wardie specimen is obscured by its displaced finspine. Most of the second dorsal fin is also missing, and only a small part of its basal cartilage can be identified behind the base of the finspine.

Anal fin. In the holotype this was described by Moy-Thomas (1936, p. 777), who identified two small cartilages behind the region of the pelvic fins and beneath the haemal arches. The specimen is broken between the cartilages, but as in the dorsal fins, cartilage appears to be more extensive than his restoration suggests, and may represent the remains of a single, proximal basal plate of the anal fin. Beneath these fragments of damaged cartilage, there are traces of one or two further poorly calcified elements. These may be radial cartilages which articulated with the basal plate.

Caudal fin. As Moy-Thomas (1936) observed, several of the haemal arches lying midway between the anal fin and the hind edge of the specimen are stout and elongated in comparison with those more anteriorly, but from this point they diminish in size caudally. These cartilages are much broader and less numerous than the neural arches above them. They are also much longer, and several of the longest (possibly up to eight or ten) may be jointed once along their length. There can be little doubt that these cartilages represent hypural elements of the caudal fin.

Moy-Thomas (1936) was uncertain about the structure of the caudal fin because of the apparent downturning of the vertebral column towards the edge of the specimen. There appears, however, to be no reason why the caudal fin of *Onychoselache* should not have been slightly heterocercal; the position in which the holotype is preserved may quite easily have been caused by flexion of the trunk muscles after death. The hypural cartilages indicate the presence of a small hypocaudal lobe, probably similar in shape to that of *Tristychius* and *Hybodus*.

Pectoral girdle. This consists of a pair of large, separate, scapulocoracoid cartilages. In RSM 1974.23.14 these have been crushed so that they now lie in the horizontal plane of the nodule, and are exposed along their entire length.

Each scapulocoracoid consists of a broad ventral coracoid region, to which the fin articulates, and a long, thin, scapular process. The proximal region of the process projects outwards slightly and has a concave lateral margin. It turns mesially through an angle of about 45° just over half-way along its length. Woodward (1924, p. 340) believed that this point, which may be termed the dorsolateral angle of the scapular process, formed the original point of articulation of the pectoral fin. It is clear, however, from the Wardie specimen (text-fig. 2) that this is not the case.

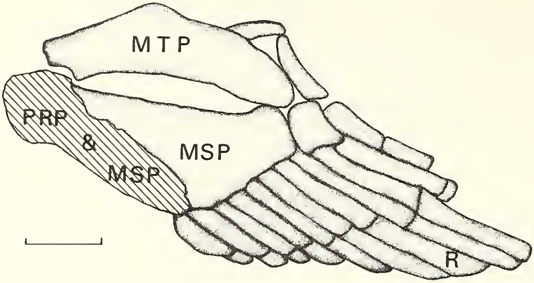
The apices of the two scapular processes in the Wardie specimen approach each other towards the midline of the body. In the Glencartholm specimen the left process lies above the level of the notochord, and it therefore seems possible that in life the apices of the two processes terminated very close on either side of the base of the first dorsal finspine.

The coracoid region is slightly better preserved in the Wardie specimen. Seen in section, it is approximately square; ventrally, a short plate runs inwards, terminating short of the midline. The lateral coracoid wall runs outwards from the base of the scapular process to develop articular processes for the three basal cartilages of the pectoral fin. Unfortunately, the articular region is damaged or hidden in both specimens. A single foramen is present on the coracoid's lateral surface in the Wardie specimen. This was undoubtedly for the passage of the brachial artery and diazonal nerves to the pectoral fin. By analogy with Recent sharks, it is probable that a further lateral foramen was present and that the two foramina lay above and below the articular region of the scapulocoracoid. A mesial foramen, by which the artery and nerves would have entered the scapulocoracoid, is not identifiable.

Woodward (1924) and Moy-Thomas (1936) disagreed about the original orientation of the pectoral girdle. Whereas Woodward considered the pectoral fin of the Glencartholm specimen to have been displaced, having originally articulated with the girdle at its broadest point, Moy-Thomas (1936) doubted that the girdle had been disturbed significantly and reconstructed the fin and girdle just as they are preserved.

Neither of these restorations of the pectoral girdle is very satisfactory, and a comparison of the two specimens suggests yet another interpretation. While the pectoral fin basals clearly have a short area of articulation on the coracoid region of the girdle, Woodward (1924) was probably correct in considering the girdle to have been displaced. In both specimens the coracoid region appears to have swung anterodorsally upon a point of rotation high up the scapular process. In the Wardie specimen this movement has been so marked that the scapulocoracoids now lie horizontally with their coracoid region crushed against the occiput of the neurocranium (text-fig. 2). Displacement of the coracoid region would also explain the condition of the branchial arches, and how the pectoral fins of both specimens have been displaced forwards. This has led, in the Glencartholm specimen, to the overlapping of the pro- and mesopterygia and, in the Wardie specimen, to the dislocation of the propterygia which now lie in front of the coracoids.

In all probability the pectoral girdle sloped posterodorsally, with the scapular process lying at an angle of about 60 to 70° to the horizontal axis of the body. Ventrally, a gap for the branchial arches would have been present between the back of the jaws and the coracoid region of the girdle.



TEXT-FIG. 3. Pectoral fin of RSM 1885.54.1. The propterygium is partially concealed by a damaged area. Scale bar = 5 mm.

Pectoral fin. The pectoral fins of the Glencartholm specimen are distorted, but enough of their structure can be determined (text-fig. 3) to show that they were very similar to those of the Wardie specimen. In the latter, both pectoral fins are exposed (text-fig. 4) with the basal and radial cartilages well spread out. Apart from the slight forward displacement of the propterygia, the basal cartilages lie much as they would have done in life.

Three large basal cartilages articulate proximally on the scapulocoracoid. All three are remarkably long, running nearly half the length of the fin, and terminating distally at approximately the same level. Their length suggests that they projected laterally into the fin well beyond the limits of the body wall. Over most of their surface the basals are quite thin, but each is stiffened by a stout marginal ridge along one side.

The propterygium is narrow and shaped like the blade of a palette knife. The proximal margin is about 2·5 mm broad and appears to have been slightly concave to receive the articular process of the coracoid. Immediately distal to the well-developed articular cotylus, the propterygium has a short neck region. Beyond this, the anterior surface develops a long, blade-like margin which curves convexly towards the bluntly pointed propterygial apex. The posterior surface of the propterygium is also convex, but considerably straighter than the anterior edge and, as it runs proximally, it thickens to form a stout marginal ridge.

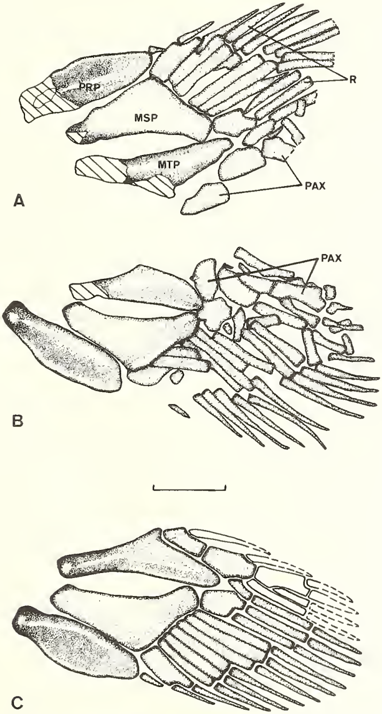
The mesopterygium is an approximately triangular cartilage, with a broad distal margin, to which the majority of the fin's radial cartilages articulate. Proximally it develops a short (about 2 mm wide) posteromesially facing articular margin for the scapulocoracoid. The anterior margin is straight, running approximately parallel with the posterior margin of the propterygium, while its thickened posterior margin is concave.

The metapterygium has a short, thick shaft proximally. It is curved so that both ends meet the mesopterygium, but the elements diverge centrally. The metapterygial apex is acute. There is a small posterodistally directed process at the broadest point of the cartilage, just over half-way from its proximal end (text-fig. 4A).

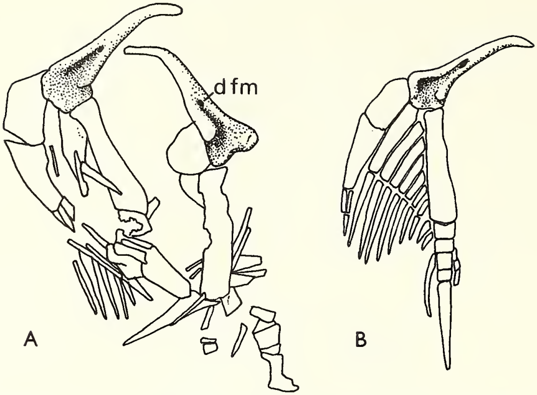
The radials of the pectoral fin probably extended to the fin margin, as at their tips there are many large denticles which probably lay along the fin's leading edge. The radials of both pectoral fins of the Wardie specimen are slightly displaced, but comparison permits an accurate reconstruction of the fins to be made.

The propterygium bears a single, short, unjointed radial, which can be seen lying displaced in the right pectoral fin. The mesopterygium bears ten radials along its lateral margin. The first eight are jointed once along their length. The proximal portions of the anteriormost two radials are fused (text-fig. 4A). While the lateral margins of the proximal parts of the next six are closely apposed, they do not appear to be fused. The final pair is jointed twice; again, their most proximal portions form a small, irregularly shaped cartilage which lies against the apical margins of both the meso- and metapterygial basals. This last pair of radials must have approached the distal apex of the fin at their tips.

The region of the metapterygial radials is extremely distorted in the Glencartholm specimen, and even in the Wardie specimen their arrangement is uncertain, although there is clearly a series of small cartilages forming a short 'axis'. Two 'axial' elements articulate with the posterodistal margin of the metapterygium; these both lie between the notch made by the posterodistal process of the metapterygium and its apex (text-fig. 4c). The second of these cartilages bore at least one, and probably two, radials along its 'pre-axial' margin near its apex. The first radial was jointed twice, the second probably only once. Both these first two 'axial' cartilages also appear to have borne a single short radial along their posterior margins. Distally, the second 'axial' cartilage articulated with a third 'axial' element, which probably bore about three radials near its apex.



TEXT-FIG. 4. Pectoral fins of RSM 1974.23.14 (counterpart). A, right fin; B, left fin; C, reconstruction of left fin. Scale bar = 10 mm. Pectoral scales omitted.



TEXT-FIG. 5. A, pelvic skeleton of RSM 1885.54.1; B, reconstruction interpreting the 'axial' cartilage as an intromittent 'clasper'.

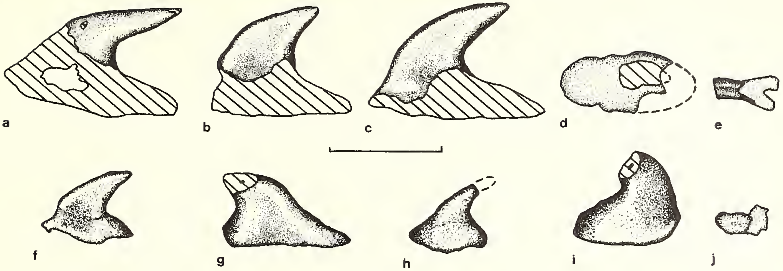
Pelvic girdle. The pelvic girdle and fins of the Glencartholm specimen lie disarticulated beneath the second dorsal fin, while those of the Wardie specimen are missing. The two halves of the pelvic girdle are unfused and much smaller than the scapulocoracoids. Each of the two cartilages has a long, curved process arising from the expanded articular region. The process probably lay horizontally within the body, projecting forwards and inwards towards the midline of the body. Its base has an elongate fossa, penetrated at one end by a foramen (text-fig. 5A), which probably allowed the diazonal nerves to reach the ventral surface of the fin.

The articular region has a pair of expanded articular facets at its antero- and posterolateral corners for the enlarged first pelvic radial and the basipterygium respectively. Between the facets, the lateral margin of each pelvic girdle cartilage is slightly concave for the articulation of the second pelvic radial cartilage.

Pelvic fin. The disarticulated cartilages of the pelvic fin are quite accurately figured by Moy-Thomas (1936, fig. 14), but a number of additional elements can be identified (text-fig. 5A). Although the condition of the pelvic fins of the Glencartholm specimen provide little objective evidence for any particular restoration of the fin, we have used the analogy of the pelvic fin of *Tristychius arcuatus* (Dick 1978, fig. 22) to propose a slightly different interpretation (text-fig. 5B) from that of Moy-Thomas (1936, fig. 15). We suggest that the specimen may be interpreted as a male with a long metapterygial axis and a long clasper cartilage.

Scales. The bodies of both specimens are generally devoid of scales. Each has a series of large, hooklike denticles (text-fig. 6) along the anterior margin of its pectoral fins. First described by Woodward (1924, p. 340), they extend from the apex of the propterygium to the distal tip of the pectoral fin. Their smooth, enamelled cusps curve mesially towards the fin insertion. The denticles have a round basal plate composed of osteodentine. The Wardie specimen also has one or two small rounded denticles along the posterior margin of the pectoral fin like those described by Woodward (1924) in the Glencartholm specimen.

In addition, there are a number of large, hooklike denticles on the heads of both specimens. These are similar in structure to those on the anterior margin of the pectoral fin, but many of their basal plates are fused together to produce multicuspid dermal rods. These are more completely exposed in

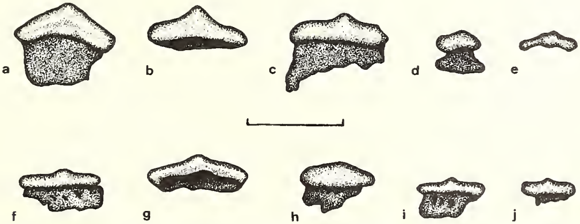


TEXT-FIG. 6. Denticles from the pectoral fins of RSM 1974.23.14 (*a*–*e*) and RSM 1885.54.1 (*f*–*j*). All are from the anterior margins of the fin, except *e* and *j*, which come from near the posterior margins. Diagonal hatching indicates broken surfaces. Scale bar = 1 mm.

the Wardie specimen, where they lie along the lateral surface of the jaws and possibly also above the gill arches (text-fig. 2); these are considered too large to be pharyngeal denticles. In the Glencartholm specimen there are single, large hook-denticles at the articulation of the jaws and above the posterior corner of the orbits.

Teeth. Teeth are preserved in both specimens and have been described in the Glencartholm specimen (Woodward 1924; Moy-Thomas 1936). There were at least fifteen tooth families in each jaw ramus, each containing four or more teeth. In the Wardie specimen the teeth lie loose near the front of the jaws. They are slightly larger than those of the Glencartholm specimen, but they have the same basic structure (text-fig. 7). In general, tooth crowns of the Wardie specimen are slightly less worn, possibly because they were positioned lingually in the replacement file and were therefore not functional.

To Woodward's (1924) description of the teeth the following may be added. All the teeth are extremely small (slightly less than 1 mm in length) and would probably be missed if they were lying isolated in matrix. Tooth roots clearly had neither a lingual nor a labial torus, but the crowns bear a small bulge on what is probably their lingual surface. This lingual button probably acted as a spacer, as in certain *Hybodus* and *Acrodus* spp. (Reif 1976).



TEXT-FIG. 7. Teeth from RSM 1974.23.14 (*a*–*e*) and RSM 1885.54.1 (*f*–*j*). Teeth (*a*–*d*) in lateral view, but it is uncertain whether lingual or labial surfaces are shown. Tooth (*e*) shows the occlusal surface. Approximate positions of others are as follows: (*f*) upper jaw, file 2 or 3; (*g*) lower file 5; (*h*) upper file 2 or 3; (*i*, *j*) upper file 8 or 9. Scale bar = 1 mm.

Dorsal finspines. Both finspines of the Glencartholm specimen are apparently in poorer condition than when they were first described. Those of the Wardie specimen are poorly exposed. Although detailed comparison with the type specimen of *T. arcuatus* is difficult, it differs from *Onychoselache* finspines in at least four respects.

(i) Size: *Onychoselache* finspines are under 40 mm long, whereas those of *Tristychius* range up to 150 mm, the majority being 70–80 mm long.

(ii) Outline in lateral view: *Tristychius* finspines are very long and slender, with gentle posterior recurvature. *Onychoselache* finspines are rather deeper anteroposteriorly, resulting in a stubby appearance. The posterior spine is fatter and more recurved than the anterior, and looks quite different from the holotype of *T. arcuatus*.

(iii) Posterior hook-denticles: a double row is present in both genera, but they are feeble in *Onychoselache* and nothing like as well developed as in *Tristychius*.

(iv) Costae: *T. arcuatus* typically has five costae per side apically, with a single costa anteriorly. *Onychoselache* has only four per side. Costal number is a variable feature in many fossil finspines, e.g. *Hybodus*, *Acrodus*, whereas in many modern examples it is constant, e.g. *Deania*, *Etmopterus*, and *Centrophorus*. Its significance is therefore uncertain in *Onychoselache*. The extent of lateral costae may be more important. In *T. arcuatus* only the anteriormost ribs reach the level of insertion; the lateral ribs terminate well above this level. In *Onychoselache* they terminate together at the level of insertion. In both forms, however, there are traces of a dermal vascular network similar to that found in Mesozoic hybodontid finspines (Maisey 1978).

Discussion. *Onychoselache* shares the following, apparently derived, features with Mesozoic hybodontids (*Hybodus*, *Acrodus*, *Asteracanthus*, etc.):

(i) finspines having posterior retrorse hooklike denticles and widely spaced lateral costae with intercostal vascular impressions;

(ii) tooth histology (Moy-Thomas 1936);

(iii) presence of enlarged head scales (although morphologically simpler in *Onychoselache* than typical hybodontid cephalic spines);

(iv) certain features of dorsal and pelvic fins;

(v) calcified ribs (Maisey 1975).

T. arcuatus is similar in features (i), (ii), (iv), and (v), but apparently lacks enlarged head spines (Dick 1978). Both fishes are here regarded as early hybodontiforms, but the following autapomorphies of *Onychoselache*, together with the differences in their finspines, seem to justify their generic separation:

(vi) dentition—low, tumid crowns and deep roots;

(vii) retrorse pectoral denticle series.

Onychoselache may be primitive in retaining plesodic pectoral fins; *Tristychius* and Mesozoic hybodontids were aplesodic.

The following features are shared by *Onychoselache*, *Tristychius*, Mesozoic hybodontids and neoselachians (including the earliest well-known form, *Palaeospinax*):

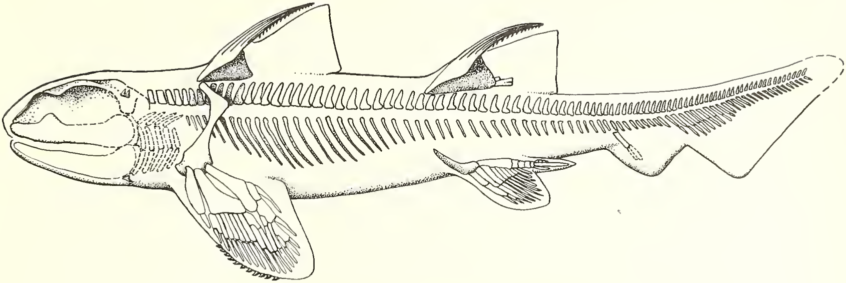
(viii) a concentrated scapulocoracoid articulation;

(ix) tribasal pectoral fins;

(x) palatoquadrate lacking a 'cleaver-shaped' quadrate region.

The retrorse pectoral denticles of *Onychoselache* are morphologically similar to posterior denticles of hybodontiform dorsal finspines, for which there is evidence of secondary fusion to the finspine trunk (Maisey 1978). It is interesting to note that the pectoral fins of a second early chondrichthyan group, the iniopterygians, are also armed (perhaps convergently) with numerous retrorse denticles anteriorly (Zangerl and Case 1973). In both *Onychoselache* and iniopterygians, pectoral scales extend down over the radials but not over the basal elements.

We concur with Woodward (1924) that the fish now known as *Onychoselache* is allied to Mesozoic hybodontids. So far we have been unable to demonstrate any derived features shared only by *Tristychius* and *Onychoselache*, and consequently refrain from placing *Onychoselache* in any family at



TEXT-FIG. 8. Restoration of *Onychoselache* skeleton.

present. Text-fig. 8 shows an outline restoration of *Onychoselache*. Reinterpretation of the pectoral fin from new material suggests that subordinal separation, as proposed by Moy-Thomas (1936, 1939), is unnecessary.

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FOOD SPECIALIZATION AND THE EVOLUTION OF PREDATORY PROSOBRANCH GASTROPODS

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Abstract. Predatory prosobranch gastropods from the Neogastropoda, Tonnacea, and Naticacea feed upon a wide variety of invertebrate prey. They are an extremely diverse trophic group comprising some twenty-six families, most of which are found at tropical or subtropical latitudes. Empirical evidence suggests that competition has been an important process in shaping the diets and habitats of related species and, over a longer time period, of the different families. Nearly all the predatory families first appeared in a massive adaptive radiation in the late Cretaceous and it is probable that the major habitat and feeding adaptations were acquired at this time. The present-day steep latitudinal gradient in diversity and the importance of Buccinidae at high latitudes were developed during and since the Miocene. In the Campanian–Maastrichtian, and perhaps for most of the Upper Cretaceous, times, predators were more diverse at higher than at lower latitudes, which is the reverse of the present-day situation. The late Cretaceous diversification of gastropods coincided with similar radiations in other predatory and non-predatory groups of marine animals. The continental fragmentation/diversity model probably best accounts for these massive changes in the composition of marine faunas.

Marine prosobranch gastropods are one of the most diverse groups of animals. They encompass a broad array of feeding types, including algal grazing, suspension and deposit feeding, grazing upon sedentary animals, parasitism, and predation, and thus may be found at several trophic levels in marine communities. The diversity and functional range of gastropods is too great for them to be treated as a unified whole, and there is clearly little interaction in competitive or evolutionary terms between gastropods belonging to different trophic groups. The object of this paper is to examine the evolution of one trophic group, the predators. This group is extremely diverse, comprising some 5000–6000 species (Boss 1971), classified into twenty-six families (after Ponder 1973). In most areas of the world at least half of the gastropods present may be classified as predators. Predators are here defined as carnivores which seek out and consume generally whole prey organisms (Curio 1976). Predatory gastropods are also numerically important in many shallow-water, particularly tropical, communities.

We know that most groups of gastropods classified today as predators did not appear until the late Cretaceous (Sohl 1964*a*) and their appearance formed part of the 'Mesozoic marine revolution' recently documented by Vermeij (1977*a*) and contributed greatly to the apparent steep increase in diversity of marine benthos towards the end of the Mesozoic described by Valentine (1969, 1973). This relatively rapid evolution of predatory gastropods, which feed today mostly upon invertebrate prey, would have had important effects upon the structure of marine benthic communities. In this paper we document the diversification of the predatory gastropod families, and attempt to relate their evolution and present high diversity to dietary and habitat specializations.

Predatory prosobranch gastropods are found today in a few families of the order Mesogastropoda, but most species are from families of the order Neogastropoda. The mesogastropod groups concerned are the superfamily Naticacea and the five families of the Tonnacea (Cymatiidae, Tonnidae, Bursidae, Cassididae, and Ficidae). Some families from both the Archeogastropoda and Mesogastropoda are carnivores, feeding by grazing upon sedentary animals such as sponges, ascidians, and coelenterates. As this behaviour is little different from grazing upon plants, these families are not considered here, although we acknowledge that there is a gradation of feeding habits from omnivorous browsers to hunting predators. Some species from the Neogastropoda and Tonnacea are not strictly predators, but in most cases they belong to families in which the

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majority of other members show predatory behaviour. The gastropod subclass Opisthobranchia also contains many predatory species, but many are either shell-less or possess very fragile shells and their geological history is difficult to evaluate.

When compared with algal grazing, for example, the act of predation involves a complex sequence of behaviour on the part of the predator. This behaviour may consist of processes of search, evaluation, pursuit, capture, immobilization, penetration, and consumption (Menge 1974; Black 1978). Predators differ in anatomical and behavioural adaptations from gastropods of other feeding categories. Ponder (1973) has documented many of the features by which predatory Neogastropods differ from other prosobranchs. These differences mainly involve modification and elaboration of the foregut and radula, including the formation of an extensible proboscis, a well-developed siphon, and the elaboration of the chemo-sensory osphradium by an increase in the surface area by folding. The nervous system is modified, with the concentration of the ganglia into the nerve ring around the oesophagus. Also with the Neogastropoda many of the major anatomical differences between the families are centred upon the feeding structures. Similar modifications are seen in the mesogastropod superfamilies Naticacea and Tonnacea. It was thought that the neogastropods were derived from the higher mesogastropods, but it is now recognized that the anatomical similarities are the results of convergence (Ponder 1973).

COMPETITIVE INTERACTIONS BETWEEN PREDATORS

In studies of groups of closely related species (guilds, taxocenes) of predatory gastropods in such families as the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975; Leviten 1976, 1978), Muricidae (Taylor 1976, 1977, 1978*a*; Bernstein 1974), Terebridae (Miller 1970), Melongenidae and Fasciolariidae (Paine 1962, 1963, 1966*a*), and Buccinidae (Nagai and Suda 1976), species have been shown to divide available ecological resources, frequently by fine differences in habitat or food. Nevertheless, in tropical environments there is often a good deal of habitat overlap between species, and Kohn (1971, p. 343) concludes that 'the strategy of specializing upon different prey species in the same microhabitat is more advantageous to the co-occurring species than specializing upon different microhabitat patch types'. Frequently, clear dietary differences exist between similar species occupying similar microhabitats. The habitats and diets amongst coexisting species are thought to have arisen over ecological and evolutionary time by competitive interactions between species, resulting in specializations which effectively partition the available resources between the coexisting species. There has been considerable controversy concerning the relative roles of competition, predation, disturbance, and other factors in organizing communities (Connell 1975, 1978). However, Menge and Sutherland (1976) point out that the relative importance of competition in organizing guild structures will change from lower to higher trophic levels; with competition expected to be much more important at higher trophic levels.

The evidence for historical competition is necessarily largely circumstantial, but recently Kohn (1978) has shown that *Conus miliaris* at Easter Island has a much broader diet than when it coexists with other *Conus* species in other parts of its geographic range. Similarly, a muricid *Cronia margariticola* has a broader diet and habitat at Hong Kong than in the more central parts of its range, where more potential predators are present (Taylor 1980). The ideas of food and habitat division can be extended more broadly to the family level. If one of the main mechanisms resulting in habitat and dietary specializations between species is the competitive interaction between taxa, then the specializations of gastropod families are the sum of the specializations of the constituent species, which have arisen over evolutionary time.

Diets of predatory gastropods

In view of the fact that many of the main anatomical differences between neogastropod families concern the structures associated with feeding and digestion, it is clear that a knowledge of the diets of these families is essential to an understanding of their adaptive radiation and evolution. However, except for the Naticacea and Muricidae, we have little direct evidence of the diet of fossil predatory gastropods and our interpretation of the habits of fossil gastropods depends upon information from related Recent species. Although the diets of some families are quite well known, for instance the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975; Leviten 1976, 1978), Fasciolariidae (Paine 1963, 1966*a*), and Muricidae (Bernstein 1974; Taylor 1976, 1978*a*), much of the information on other families is widely disseminated throughout the literature and is often highly anecdotal in nature. The detailed quantitative information assembled for Conidae by Kohn and his associates is unequalled in any other family. The available information on the diets of predatory prosobranchs is summarized in Table 1. For many families the data are woefully sparse, and for some, namely the

TABLE 1. Major prey items in the diets of predatory prosobranch families. The most important prey for each family in heavy type.

major prey predator families	Gastropods	Bivalves	Sedentary polychaetes	Errant polychaetes	Sipunculids	Enteropneusts	Decapod crustacea	Small crustacea	Cirripedes	Echinoids	Asteroids	Holothurians	Ophiuroids	Ascidians	Priapulids	Brachiopods	Hydroids	Corals	Fish	Foraminifera	Ostracods	Algae	Carrion
NATICACEA	✱	✱																		*	*		
CYMATIIDAE	*	✱	*	*			*			*	*	*		*		*						*	*
BURSIDAE			*	✱	*					*	*		*										
CASSIDIDAE										✱													
TONNIDAE												✱											
FICIDAE										*													
MURICIDAE	✱	✱	*	*	*		*	*	✱	*			*			*		*					*
CORALLIOPHILIDAE																		✱					
COLUMBELLIDAE			*	*				*						*			*					*	*
BUCCINIDAE	*	✱	✱	✱	*		*	*	*	*				*	*								✱
MELONGENIDAE	✱	✱																					
NASSARIIDAE			*	*					*														✱
FASCIOLARIIDAE	✱	✱	✱						*														*
VASIDAE			✱	*	✱																		
VOLUTIDAE	✱	✱																					
OLIVIDAE	*	✱	*																	*	*		*
HARPIDAE							✱																
MARGINELLIDAE	✱																			*			
MITRIDAE	*				✱																		
VEXILLIDAE	*																						
CANCELLARIIDAE	*																						
TURRIDAE			✱	*																			
CONIDAE	✱	*	✱	✱		*													✱				
TEREBRIDAE			✱	✱		*																	

Ficidae, Cancellariidae, and Columbariidae, are virtually non-existent. However, for the other families some broad dietary patterns emerge which are instructive in considering the evolution of predators.

The mesogastropod families Cassididae, Tonnidae, Bursidae, and Cymatiidae are the only families which regularly eat echinoderms; the Cassididae eating echinoids (Moore 1956; Hughes and Hughes 1961), the genus *Charonia* of the Cymatiidae eating asteroids, and holothurians (Percharde 1972; Thomassin 1976), the Tonnidae eating holothurians (Grange 1974), and the Bursidae eating, amongst other things, ophiuroids, echinoids, and crinoids (Taylor 1978*a*). Crustacea are eaten by only a few families; the Harpidae feed upon decapods (Rehder 1973), whilst a few species of Buccinidae, Nassariidae and Muricidae regularly take smaller free-living crustacea. Only the Buccinidae and Muricidae eat barnacles. Sipunculids are the main prey of the species of Mitridae so far studied (Kohn 1970; Taylor 1976, 1978*a*), but are eaten by only a relatively small number of species from other families.

Polychaetes are amongst the most diverse groups of macroinvertebrates and they figure extensively in the diets of predatory gastropods. The worms differ considerably in size, habits and mobility and this variety is reflected in different predatory gastropod families tending to take different types of polychaete prey. Some families eat only sedentary polychaetes, such as the Sabellidae and Terebellidae, others take the predatory errant groups such as the Nereidae and Eunicidae. Some families are polychaete specialists, and many species of the families Conidae, Terebridae and Turridae eat polychaetes exclusively, whilst species in other families may eat polychaetes regularly but not exclusively.

Molluscs are also eaten by many gastropod families and here again there is a broad variation in the type of mollusc taken depending upon the size, mobility, and habits of the prey and predator. Thus, although the Muricidae generally eat sedentary molluscs such as epifaunal bivalves and sedentary or slow-moving gastropods, other families, such as the Naticidae, Cymatiidae, Volutidae, and Conidae can feed upon more mobile gastropods. There is some overlap in diet of these dominantly predatory families with the browsing carnivores of the Archaeo- and Mesogastropoda. For instance, species of the Neogastropod family Coralliophilidae feed exclusively upon coelenterates (Robertson 1970; Hadfield 1976) as do a few species of Muricidae (Taylor 1976, 1978*a*) and Columbellidae (Bandel 1974). Some Cymatiidae and Vexillidae feed upon ascidians (Laxton 1971; Morton and Miller 1968), whilst some Columbellidae and *Apollon natator*, a species of Cymatiidae, feed upon algae (Bandel 1974; Marcus and Marcus 1962: Taylor 1980). Additionally Scheltema (1964) reports *Nassarius obsoletus*, a species with a crystalline style, as a deposit feeder.

Many gastropods will feed upon carrion when available; the best-known families having this habit are the Nassariidae and Buccinidae (Brown 1971; Lloyd 1971; Taylor 1978*b*). However, many observations have been made in unnatural conditions such as aquaria and baited traps (Arnaud 1970) and the natural diet of some of the species, such as *Buccinum undatum*, also includes a wide variety of live prey, particularly polychaetes (Taylor 1978*b*). Similar observations have been made upon the genus *Bullia* (Nassariidae) in which carrion is taken when available (Brown 1971), but gut samples of *Bullia mauritiana* reveal a diet consisting largely of live-taken polychaetes and small, sand-dwelling crustacea. Some *Conus* species are well known for their ability to catch small fish, especially gobies (Kohn 1959; Kohn and Nybakken 1975). Unexpected prey items have been reported for some predators, for example *Priapulus* is eaten by *Neptunea antiqua* (Taylor 1978*b*) and dogfish egg cases bored by *Natica* (Ansell 1961). The prey most commonly taken by predatory gastropods are polychaetes and bivalve molluscs which are eaten by species from twelve and nine families respectively. The Cymatiidae, Bursidae, Muricidae and Buccinidae might be considered the more generalist families in taking a wide variety of major prey categories, whilst other families such as the Mitridae, Cassididae and Turridae appear to be relatively specialized.

Methods of attack

An extensive array of behavioural and mechanical devices is used by predatory gastropods for immobilizing and gaining access to their prey.

Some predators merely thrust their proboscis into their prey, and down the tubes of animals such as sedentary polychaetes or vermetid gastropods, or wait for bivalve prey to open before inserting their proboscis. Species of Melongenidae, Fasciolariidae, Buccinidae, and some Muricidae wedge the lip of their shell aperture between the valves of bivalve prey allowing the insertion of the proboscis; Nielsen (1975) illustrates this for *Buccinum undatum*. This behaviour has been elaborated in some Melongenidae and Muricidae where species of *Busycon* and *Muricanthus fulvescens* chip the edges of thicker-shelled bivalve prey until there is sufficient space to insert the shell lip and proboscis between the valves (Carriker 1951; Paine 1963, 1966*a*; Wells 1958). In the Volutidae (Ponder 1970) and some Olividae (Marcus and Marcus 1959; Olsson and Crovo 1968) the bivalve or gastropod prey is enveloped in the large foot until apparently asphyxiated and partially open. In the Harpidae the crustacean prey is held in the propodium and foot, and a sticky fluid released which envelops and immobilizes the prey. The drilling of shelled prey is known from three predatory prosobranch taxa, the Naticacea, Muricidae, and the Cassididae. Day (1969) suggests that *Argobuccinum* of the Cymatiidae could drill holes, but there is no evidence of this from actual feeding observations. Similarly, another cymatiid, *Monoplex australasiae*, has been reported as drilling bivalves, but this was not confirmed in a detailed study by Laxton (1971). Some species of the mesogastropod family Capulidae can also drill bivalves (Orr 1962; Matsukuma 1978) but these species do not kill the bivalve and can be classed as parasites. The drilling process in the Muricidae has been reviewed by Carriker and van Zandt 1972, and Carriker and Williams 1978, and in the Naticidae by Ziegelmeier (1954). Drilling of echinoid tests by the Cassididae has been shown by Hughes and Hughes (1971). The shell-drilling process in the Muricidae and Naticacea involves mechanical radular scraping combined with chemical secretions from the accessory boring organ, in the foot of Muricidae and in the proboscis of Naticacea. A recent review by Carriker and Williams (1978) suggests that a combination of enzymes, inorganic acid, and chelating agents is involved in the chemical phase of shell penetration by both naticid and muricid gastropods.

The use of toxic secretions to immobilize prey is known in several families; some species of Cymatiidae squirt a venom at their mollusc prey (Houbrick and Fretter 1969), and the vexillid *Thala floridana* uses a toxic secretion to immobilize prey after the proboscis has touched the prey (Maes and Raeihle 1976). The toxoglossan families Turridae, Terebridae, and Conidae utilize a toxic secretion produced by the venom gland. The venom is injected into the prey following puncture of the victim by the dart-like radula teeth (Kohn 1959; Pearce 1966). In some Terebridae there is no venom apparatus, and in *Terebra gouldii* the proboscis is applied closely to the enteropneust prey and rapidly everted (Miller 1975). In some groups, particularly those feeding upon errant polychaetes, such as the Buccinidae, Muricidae, Bursidae, and Vasidae the methods of attack and prey immobilization are unknown, although venoms have been reported (Pearce and Thorson 1967; Fänge 1958).

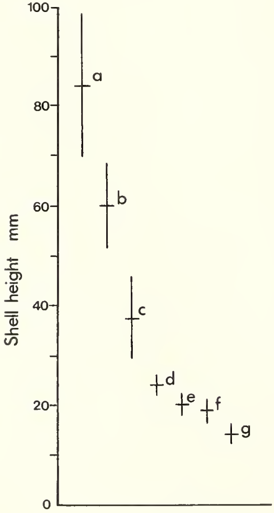
Habitats of predators

Studies of coexisting similar species of predatory gastropods such as the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975), Melongenidae and Fasciolariidae (Paine 1962, 1963), and Muricidae (Taylor 1976, 1978*a*; Bernstein 1974) have shown differences in habitat occupation patterns between potentially competing species. These differences involve such factors as substrate preferences, zonation along some intertidal gradient, such as wave exposure or length of emersion, differences in microtopography, or by size of the predator, allowing exploitation of different sizes of microhabitat. Although most studies have been in the tropics, Nagai and Suda (1976) show clear habitat separation amongst similar species of *Neptunea* in the Bering Sea, and Okutani (1968) shows depth partitioning amongst species of Volutidae and Buccinidae in Sagami Bay, Japan. Some circumstantial evidence for broader-scale partitioning comes from the two toxoglossan families Terebridae and Conidae. Both families are probably descended from a common ancestor; they have similar food-gathering apparatus and commonly occur at the same localities. However, the two families show quite different habitat preferences; the Terebridae are entirely confined to sandy substrates, whilst the Conidae occur in a number of habitats including rubble, hard reef-platform, and coral areas, with only a few species of *Conus* occurring in the same habitats as the Terebridae.

Most of the twenty-six families of predatory gastropods live partly upon soft substrates; only thirteen families contain species which regularly occur upon hard substrates, and of these only the Coralliophilidae, which live upon skeletonized coelenterates, are exclusive to hard substrates. The Muricidae is the most diverse family which regularly inhabits hard substrates; its large subfamily Thaiinae has diversified extensively upon rocky intertidal shores where the species are important members of food webs throughout the world (Connell 1961, 1970; Paine 1966*b*; Taylor 1976; Luckens 1970; Phillips 1969). Other families containing species which regularly occur upon hard substrates are the Cymatiidae, Bursidae, Buccinidae, Columbellidae, Fasciolariidae, Mitridae, Vexillidae, Turridae, and Cassididae. By contrast, the families Olividae, Terebridae, Harpidae, Ficidae, Tonnidae, and Naticidae are confined exclusively to soft substrates. Species of the Marginellidae and Buccinidae are found in freshwater habitats in south-east Asia (Jutting 1956; Brandt 1974).

Size variations in predators

Predatory gastropods exhibit a large variation in size from the large volutid *Melo* (500 mm) and the melongenid *Syrinx* (700 mm) down to tiny Turridae at 1–4 mm. Morphological differentiation between guilds of coexisting species presumably reflecting resource partitioning has often been inferred to be the direct evolutionary consequence of competition. Size differences between predators may allow division of resources by size, smaller predators in general taking smaller prey items which are generally more abundant and often occur in monospecific aggregations. Large predators, which tend to feed upon larger prey, are usually less specialized in diet (Schoener 1974) as demonstrated for *Pleuroploca* in the Fasciolariidae by Paine (1963). Size differences between coexisting species of intertidal muricid gastropods, probably reflecting the dietary differences, are illustrated in text fig. 1;



TEXT-FIG. 1. Shell height (mean and standard deviation) of seven coexisting species of muricid gastropod on a shallow sublittoral rocky shore in Tolo Channel, Hong Kong (from Taylor 1980). Species a. *Chicoreus microphyllus*; b. *Chicoreus brunneus*; c. *Mancinella echinata*; d. *Drupella rugosa*; e. *Drupella contracta*; f. *Morula spinosa*; g. *Cronia margariticola*.

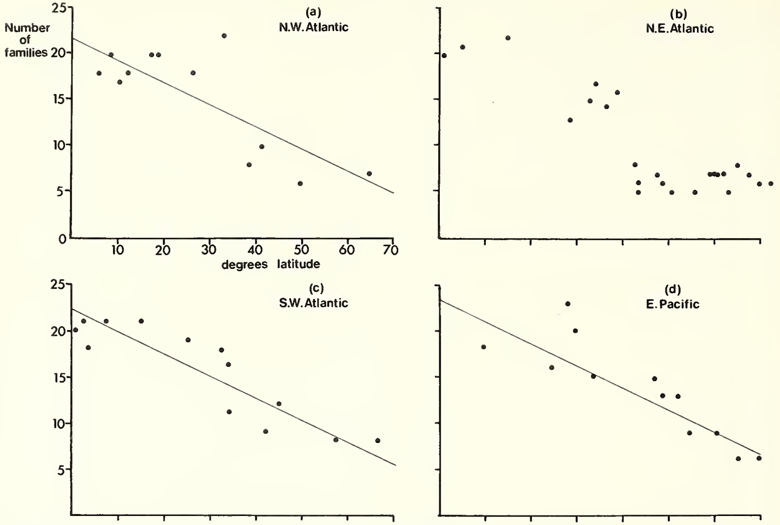
although other guilds of species in other predatory gastropods, for example the Conidae, need not show such differences (Leviten 1978). Size differences between taxa may allow greater division of habitat space and small species can occupy microtopographic features of the substrate unavailable to larger species. Large species frequently forage over a number of habitat types, each representing the sole habitat for smaller species.

Other selection pressures may be influencing these size adaptations, for small species are vulnerable to a greater range of predators and environmental stresses than larger species, and the latter may effectively 'grow out' of predation pressure. In *Conus* species, small body size is a liability in sublittoral habitats where predation is intense and large body size is a disadvantage on intertidal benches where predation is less but wave action is strong and shelter becomes important (Leviten 1978). Some families such as the Volutidae, Melongenidae, Muricidae, Vasidae, and Tonnidae contain many large species, whilst others such as the Marginellidae and Turridae are dominated by rather small species. In other families there is more size variation, but the over-all size characteristics of the various families tend to reflect the major niche dimensions of the particular family.

DISTRIBUTION OF PREDATORY GASTROPODS

We know that in common with many other animal groups (Stehli 1968) there are strong latitudinal gradients in the species and family diversities of predatory gastropods, and also that there are large changes in the composition of predatory faunas with latitude (Taylor and Taylor 1977). Hence, in order to interpret the changes in diversity and taxonomic composition of predatory gastropod faunas during and since the Cretaceous we must examine the present-day patterns of gastropod distribution in some detail. It has recently been argued by Osman and Whitlach (1978) that the latitudinal species diversity gradient is a function of the spherical shape of the Earth. They pointed out that the area of the Earth's surface occupied by the tropics and subtropics is much greater per degree of latitude than the extratropical zones, and will thus support more species. However, for continental shelf habitats this argument does not hold, because most continental margins trend north–south and the shallow shelf areas are actually greater at higher than at lower latitudes. Osman and Whitlach (1978) have further argued that because of the shape of the Earth there is greater spatial separation and hence greater isolation of tropical faunas, which encourages higher diversity. Higher-latitude faunas are supposed to be less spatially separated, with consequently greater faunal mixing and lower diversity. In fact, tropical faunas exhibit great similarity over large areas, witness the enormous, but uniform Indo-Pacific marine province extending from East Africa to the central Pacific. Moreover, Arctic faunas are not as uniform as might be expected; for instance, Clarke (1974) has documented the considerable east–west changes in the molluscan faunas of the northern North Atlantic and Baffin Bay.

Gastropod faunas were examined from localities throughout the world, but in the interests of simplicity only the distributions for north–south trending continental margins are presented here. The data used were extracted from monographs and faunal lists which vary in quality and completeness, but the over-all trends are clear. Predictably, the number of families and species of predatory gastropods show a strong latitudinal gradient increasing towards the Equator. This trend is illustrated in text-fig. 2*a–d* for a number of continental margins for which adequate faunal information is available. A rather rapid change in family richness at around latitude 40° N. is particularly marked in the western and eastern Atlantic and this has been discussed by Taylor and Taylor (1977). The two other continental margins examined show a more even diversity gradient. The diversity of species within families was estimated in two ways, by the Shannon diversity index H′ (Pielou 1977) and by the rarefaction method (see Raup 1975). Both H′ and rarefaction curves show similar trends, with a steep decline in diversity towards higher latitudes (text-fig. 3*a–d*). In the eastern Atlantic the rarefaction curves show two groupings, with a high-diversity group from sites south of latitude 35–40° N. and a low-diversity group from stations north of this latitude (Taylor and Taylor 1977, fig. 4). Similar groupings are seen in the western Atlantic, but more gradual changes in diversity are seen on the Pacific coast of north America and upon the Atlantic coast of South America.



TEXT-FIG. 2*a–d*. Variation in the numbers of Recent predatory gastropod families with latitude along four continental margins. Lines are linear regressions. Source of data:

a. NW. Atlantic: Abbott (1958), Altena (1975), Coomans (1962), Dall and Simpson (1901), Houbrick (1968), Johnson (1915), Jong and Kristenson (1965), Macpherson (1971), Nowell-Usticke (1959), Olsson and McGinty (1958), Perry and Schwengel (1955), Porter (1974), Provancher (1891).

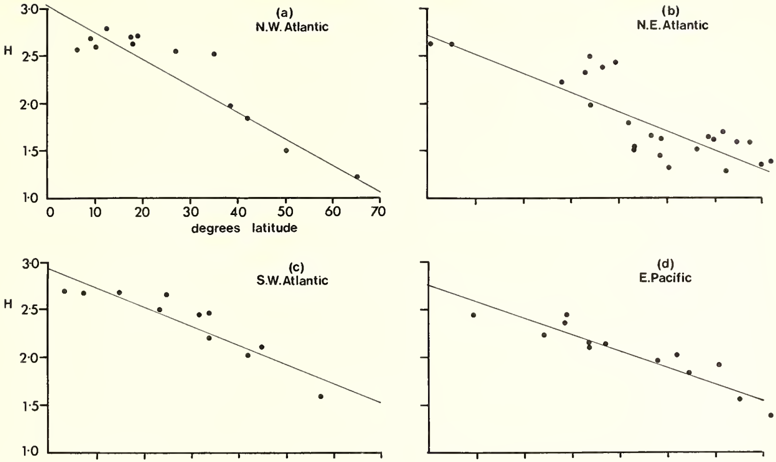
b. NE. Atlantic: Bellon-Humbert (1971), Cadée (1968), Cornet and Marche-Marchad (1951), Dautzenberg (1898), Dautzenberg and Durouchoux (1913), Fischer (1899), Geerts (1969), Hägg (1905), Knight (1901), Leche (1878), MacAndrew (1850), MacAndrew and Woodward (1864), Marche-Marchad (1958), Marine Biological Association (1957), Nobre (1932, 1937), Norman (1879, 1902), Ohdner (1915), Pasteur-Humbert (1962), Rendall (1956), Sneli (1974), Sparck and Thorson (1933), Thorson (1941, 1944), Tomlin (1923), Tomlin and Shackleford (1914, 1915).

c. SW. Atlantic: Barattini (1951), Carcelles (1950), Castellanos (1967), Matthews and Kempf (1970), Powell (1951), Rios (1975), Scarabino (1977).

d. E. Pacific: Adams (1852), Bernard (1970), Bishop and Bishop (1973), Dall (1874), DuShane and Poorman (1967), Eyerdam (1924), Keen (1964), MacGinitie (1959), McLean (1961, 1969), Oldroyd (1924–1927), Smith and Gordon (1948), Willett (1919).

Faunal composition

On all the north–south gradients there is a distinct change in faunal composition at the family level. At high latitudes two families, the Buccinidae (as Buccinulidae in many Antarctic references) and the Turridae, contain proportionally the highest number of species, whilst at lower latitudes species are much more equitably distributed amongst more families. The rise in importance of the Buccinidae along a number of north–south continental margins is shown in text-fig. 4*a–d*. At high latitudes approximately 45% of predatory species belong to the Buccinidae, but at low latitudes they form only about 5% of species. There is a rapid change in the slope of the curves at around latitudes 35–40° N. and S. The comparative success of the Buccinidae at high latitudes has been attributed to their

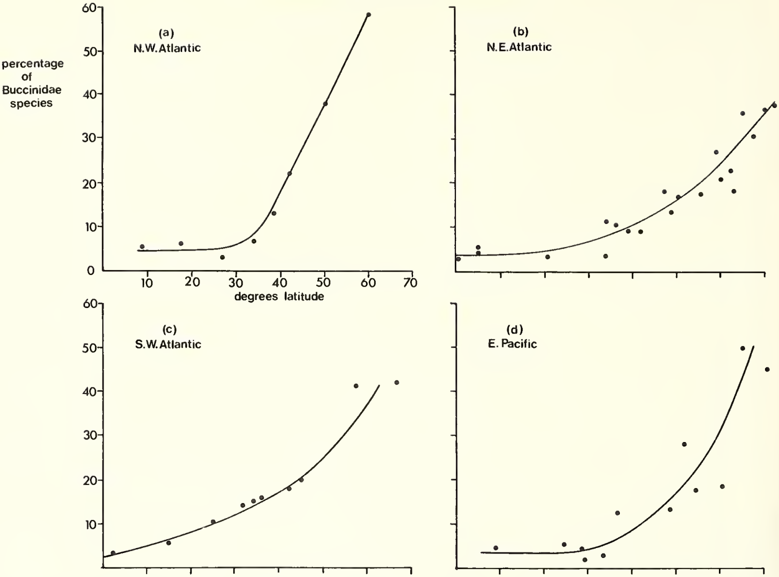


TEXT-FIG. 3*a–d*. Variation in the diversity of species (H′, Pielou 1977) within Recent predatory gastropod families along four continental margins. Lines are linear regressions. Data as for text-fig. 2*a–d*.

generalist feeding habits (Taylor 1978*b*). The family Turridae is relatively diverse at all latitudes but together with the Buccinidae it is the most important predatory family at high latitudes (text-fig. 5). The few data that are available suggest that the Turridae feed mainly upon deposit-feeding polychaetes (Pearce 1966; Taylor 1979; Shimek 1977). Thus, although specialized, they are exploiting a stable resource in a strongly seasonal environment while the food-supply to algal grazers or suspension feeders is strongly limited during the winter months.

Depth distribution

As well as the latitudinal differences in distribution between predatory families there are pronounced differences along the depth gradient. The total number of prosobranch gastropods decreases into deeper water and this is also true of the predatory species. Clarke (1962) catalogued the species recorded from abyssal depths (greater than 1828 m, originally 1000 fms.) and although seventeen families of predatory gastropods have been recorded, six of these are represented by a single species. Most of the other species belong to just a few families with 58% of them belonging to the Turridae, 13% to the Buccinidae, 7% to the Naticacea, 5% to the Muricidae, and 4% to the Tonnidae. This general pattern is reflected in individual samples, for instance on the Deutschen Tiefsee Expedition (Thiele 1925), in virtually all the samples taken below 500 m at least 50% of the species are Turridae. A similar pattern was described by Okutani (1968) in a survey of archibenthal and abyssal gastropods from Sagamai Bay, Japan, where 34% of the predatory species belong to the Turridae and 24% to the Buccinidae. As yet, little taxonomic information is available from recent deep-sea work using more efficient sampling techniques, but Rex (1976) reports that between 478 and 4862 m in the western Atlantic 74·5% of predatory prosobranch species belong to the Turridae. Predator diversity increases to a depth of about 2500 m and then declines towards the abyssal plain where most gastropods are deposit feeders. Knudsen (1964) reviews the gastropods found from hadal depths (below 6000 m) where only fourteen species are known and of these six are predators belonging to the Naticidae, Cancellariidae, and Buccinidae. The Turridae, so diverse at abyssal depths, are notably absent.



TEXT-FIG. 4*a–d*. Latitudinal variation in the percentage of Buccinidae species out of the total predatory gastropod fauna for Recent samples along four continental margins. Curves fitted by eye. Data extracted from references cited in text-fig. 2*a–d*.

ORIGIN OF PREDATORY GASTROPODS

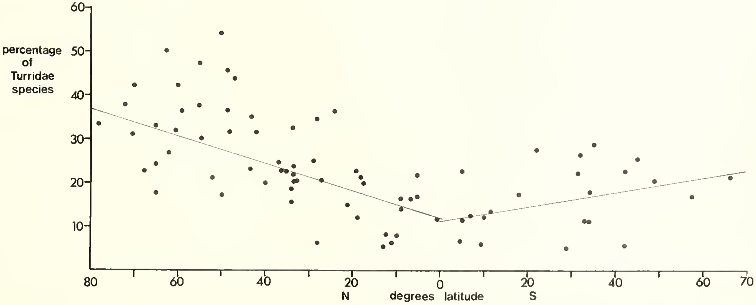
The predatory prosobranch gastropods as discussed in this paper comprise three major groups, the two superfamilies Naticacea and Tonnacea of the Mesogastropoda and the families of the order Neogastropoda. The phylogenetic relationships between and within these three groups are imperfectly understood, but our ideas concerning the origins and relationships of the three groups are briefly reviewed following.

Naticacea. The Naticacea have the longest history of any of the predatory groups and are known back to at least the lower Jurassic. The superfamily is characterized by unornamented, globular, rather featureless shells; this makes their ancestry difficult to ascertain. Moreover, the anatomical features of living species have so far given no real clues to relationship (Fretter and Graham 1962). The Triassic to Jurassic family, the Coelostylinidae, is a probable stem group for many later mesogastropod families, and includes many species with globular, unsculptured shells, very similar in morphology to those of the naticids. We believe that the naticids, along with several other groups of mesogastropods, may have had their origins with this family.

Tonnacea. The Upper Jurassic–Cretaceous family Columbellinidae have shells with distinct anterior and posterior apertural canals, frequently with denticulate outer and inner apertural lips. Upper Jurassic members of the family vary from forms with constricted and then flared apertures, resembling Cymatiidae, through others where the internal shell layer covers one side of the outside of the shell, to an extreme where in the adult state the outer shell layers are completely covered by inner shell layers, indicating extensive reflexing of the mantle over the dorsal surface of the shell. Columbellinids from the Aptian and Albian include forms with shell characters resembling those of the Cymatiidae, Bursidae, and Cassididae and the derivation of these families from the Columbellinidae is probable. The Cypraeacea (excluding the Triviidae and Eratoidae) were probably derived from those columbellinids in which the extensive reflection of the mantle occurred. The Columbellinidae were in turn probably derived from *Diarthema*, a Middle Jurassic genus placed in the Strombacea, which as well as having many aporrhaid features, has incipient anterior and posterior canals, an apertural constriction, and an extension of the inner shell layer to form an expanded inner lip. The Columbellinidae probably thus shared a common ancestor with the Strombacea, and in turn gave rise to the Cypraeacea and Tonnacea.

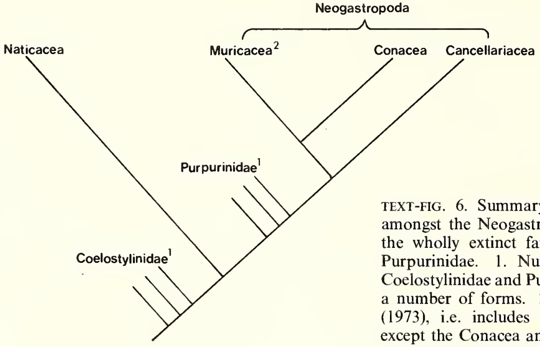
Neogastropoda. In his broad survey of the Neogastropoda Ponder (1973) was unable to find anatomical justification for the present superfamilial divisions of the Neogastropoda. His revised classification, which has yet to gain acceptance, proposes three broad divisions which he calls superfamilies; the Conacea, comprising the toxoglossate families Terebridae, Turridae, and Conidae; the Cancellariacea with one family and the Muricacea consisting of all the other seventeen families. The three superfamilies differ considerably in the organization of the foregut, and in Ponder's view each evolved separately from an early neogastropod ancestor before the elongation of the snout to form a proboscis. Although the Neogastropods have traditionally been regarded as originating by progressive elaboration from the higher Mesogastropods such as the Tonnacea, Ponder (1973) presented clear evidence that indicates that the two groups have independent origins and to some extent show parallel development of anatomical features. On the basis of a number of anatomical characters shared between the Neo- and Archaeogastropoda, but not the Mesogastropoda, Ponder proposed that the Neogastropoda were derived from an Archaeogastropod or primitive Mesogastropod ancestor. Following Knight *et al.* (1954), Ponder thought that the extinct family Subulitidae had some of the characters required in an ancestral Neogastropod. These included an anterior notch, sometimes a columellar fold and a non-nacreous shell. Knight *et al.* (1954) derived the Nerinacea, Muricacea, and Buccinacea from the Subulitacea and suggested that in turn the Nerinacea gave rise to the Volutacea and Conacea. The link suggested between the Neogastropods, Subulitacea, and Nerinacea seems to depend mainly on the presence of an anterior canal and columellar folds. The anterior canal has certainly evolved more than once amongst unrelated groups of prosobranchs such as the Cerithiacea, Purpurinidae, and Tonnacea, and although an important feature it is not in itself sufficient reason for linking the groups. In fact there is no certainty of the relationship between the Nerinacea and the Subulitacea. The Nerinacea typically have strong columellar folds and an opisthobranch-like opisthocline aperture. The internal folds could be interpreted as having supported a channelled ciliated mantle resembling the mantle caecum and similar structures in the opisthobranchs (Fretter and Graham 1962). The heterostrophic protoconch reported for some Nerinacea (Bigot 1896) which might further support their placement in the Opisthobranchia, has not been confirmed; nevertheless, this character has been independently evolved in other gastropods.

A more likely derivation of the Neogastropods would seem to us to lie in the middle Triassic to Upper Cretaceous family the Purpurinidae, many of which have an anterior notch and a range of apertural shapes and



TEXT-FIG. 5. Variation in the percentage of Turridae species in the total predatory gastropod fauna with latitude for Recent faunas. Lines are linear regressions. Data mainly from sources listed in text-fig. 2*a–d*.

shell sculpture comparable to that of the Neogastropoda. As with the Naticacea, it seems most likely that the Purpurinidae are an offshoot of the Coelostylinidae. We suggest that the Cancellariacea, Conacea, and Muricacea (*sensu* Ponder 1973) share a common ancestor in the Purpurinidae. An initial branching separated the Cancellariacea, with their distinctive anatomical features and radula from the common ancestor of the Muricacea and the Conacea (text-fig. 6). Some Purpurinidae are very similar in shell morphology to cancellariids. The Muricacea and Conacea have a number of features in common and some Turridae show close resemblances in shell morphology and anatomical characters, other than the anterior alimentary system, with the Fasciolariidae. However, the second major split in the evolution of the Neogastropods involved the separation of the Conacea from the Muricacea, the two groups differing mainly in the organization of the anterior alimentary system. The common ancestor of the two families should have possessed five teeth in each radular row, a feature found in some living Turridae but not in the Muricacea which have three teeth or less.

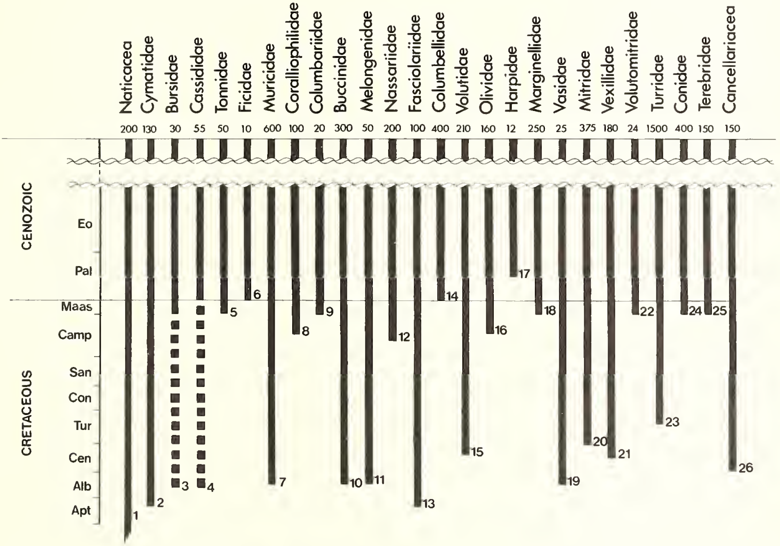


TEXT-FIG. 6. Summary of possible relationships amongst the Neogastropoda and Naticacea with the wholly extinct families Coelostytinidae and Purpurinidae. 1. Number of branches for the Coelostylinidae and Purpurinidae merely indicates a number of forms. 2. Muricacea *sensu* Ponder (1973), i.e. includes all Neogastropod families except the Conacea and Cancellariacea.

ANALYSIS OF FOSSIL GASTROPOD FAUNAS

The first records of species recognizable as belonging to the various predatory families are shown in text-fig. 7 together with the relevant references. The assignment of some of the early species to families is rather subjective, for members of related families tend to resemble each other more closely, than later in their evolutionary history. Correct assignment to a family often depends upon tracing the details of species lineages, and in many cases this information is just not available for Cretaceous gastropods. Modifications to the ranges shown in text-fig. 7 are to be expected but the broad pattern of diversification is unlikely to be greatly altered. More interesting perhaps than recording the first appearance of the different families, is the pattern of the incorporation of these families into faunas and communities and how these patterns have changed with time. For instance, some families appeared relatively early in the Upper Cretaceous but were neither diverse nor numerically very important until much later, whilst other families apparently diversified rapidly. A basic assumption made here is that fossil gastropods which have similar shell morphology to their living relatives had similar habits. Although studies of the functional morphology of the gastropod shell are still in their infancy, Vermeij (1973) and Linsley (1977) have shown a strong relation of shell shape to habit. Moreover some characters of shell shape are related to modifications of the food-gathering apparatus; for example, the fish-eating species of *Conus* generally have broad, flared apertures when compared with polychaete-eating species. More direct evidence comes from the appearance of muricid-like drill holes in bivalves of the Albian, at the same time as the first unambiguous muricid gastropods (see below) which confirms the assumption.

Data for the study were obtained from many monographs and faunal lists, and the sources are listed with each diagram. The data vary considerably in quality and completeness, a problem particularly acute in fossil faunas from both very high and very low latitudes. However, some broad patterns emerge which transcend this rather variable data. Lists of faunas were examined from the Miocene, Eocene, and the Cretaceous, time units selected as giving adequate sampling to establish the broad patterns of predatory gastropod evolution. Some reassignment of species to families was necessary, particularly with older literature. Families were used as the basic taxonomic unit, for Sepkoski (1978), using models and empirical evidence, has shown that the higher taxa parallel the patterns and kinetics of species diversification even when the information loss due to incomplete sampling of the fossil record masks these patterns in the species themselves. Palaeolatitudes were estimated using the palaeocontinental maps of Smith and Briden (1977).



TEXT-FIG. 7. First appearance and stratigraphic ranges of predatory prosobranch families from the Aptian onwards. Numbers at the foot of the bars refer to references and notes below; numbers at the head of the bars give an approximate estimate of the number of Recent species in each family (partly from Boss 1971). 1, Sohl (1969); 2, Morris and Cleevely (unpub.); 3, Morris and Cleevely (unpub.); 4, Morris and Cleevely (unpub.); 5, Wenz (1938); 6, Wenz (1938); 7, Sohl (1969) and others; 8, Sohl (1964*a*); 9, Darragh (1969); 10, Morris and Cleevely (unpub.) Buccinidae are probably a polyphyletic group; 11, Morris and Cleevely (unpub.); 12, *Buccinopsis* in Sohl (1964*a*), Nuttall *pers. comm.*; 13, Morris and Cleevely (unpub.); 14, Glibert (1973); 15, Stephenson (1952); 16, Sohl (1964*a*); 17, Rehder (1973); 18, Ponder (1973); 19, Morris and Cleevely (unpub.) Vasidae may be a polyphyletic group; 20, Cernohorsky (1970), the designation of Cretaceous species to this or the following family is rather subjective; 21, Cernohorsky (1970); 22, Cernohorsky (1970); 23, Stoliczka (1867–1868); 24, Powell (1966); 25, Powell (1966); 26, Stephenson (1952), if *Palaeadmete* can be accepted as a Cancellariacean.

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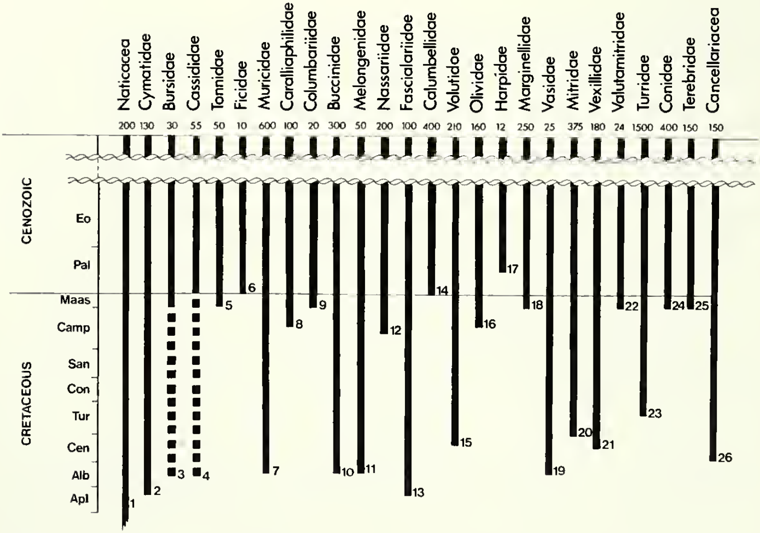

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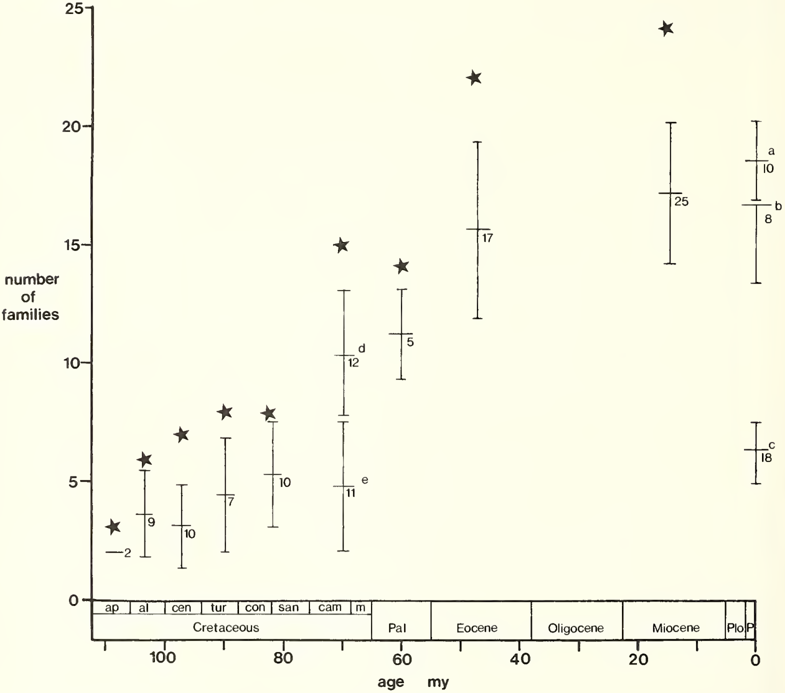
Diversity changes with time

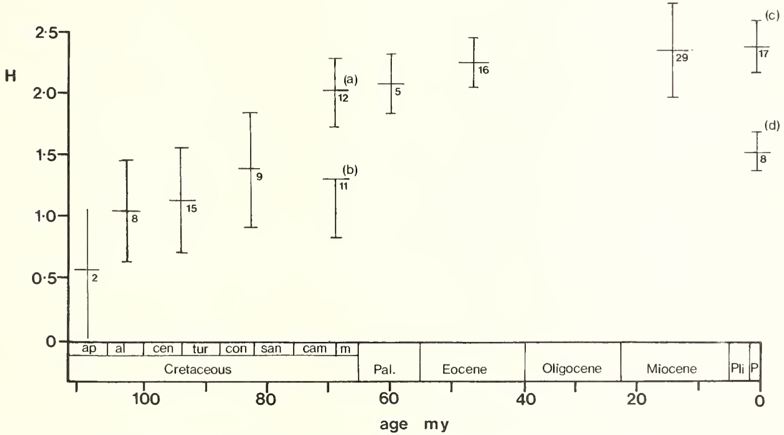
The diversity of predatory gastropod families and of species within families from various faunas from the Upper Cretaceous to the present day is shown in text-figs. 8 and 9. There is a steady increase in diversity from the Aptian to the Turonian, with a further larger increase in the Campanian-Maastrichtian. This steep increase continues to the Eocene (few faunas were sampled for the Paleocene) and then flattens off to the Miocene and Recent. As will be shown below, the diversities of low-latitude predatory faunas in the Campanian-Maastrichtian are low, and are thus shown



TEXT-FIG. 8. Number of predatory gastropod families in faunas from the Upper Cretaceous to the Recent. Data have been grouped for the Cenomanian–Turonian, Coniacean–Santonian, and Campanian–Maastrichtian stages. In view of the large diversity differences between high and low latitudes in the Campanian–Maastrichtian, the faunas have been split into two groups: (*d*) faunas from north and south of palaeolatitude 23·5° N. and S.; and (*e*) faunas from within palaeolatitudes 23·5° N. and S. Three Recent points are shown for comparison: (*a*) NW. Atlantic S. of 40° N.; (*b*) NE. Atlantic S. of 40° N.; (*c*) NE. Atlantic N. of 40° N. Bars show means, standard deviations, and the number of faunas sampled, except for the Aptian, which shows the mean and range. Stars indicate the maximum number of families recorded in any fauna of that age. Data sources as for text-figs. 2*a*–*d*, 11*a*–*d*, and 12*a*–*b* with the additions of Nagao (1934) and Cleevely (unpub.) for the Aptian.

separately from the extra-tropical faunas. Several Recent values are included because of the strong latitudinal variations which occur today. The diversification appears to take place in two phases, the first from the Albian to the Santonian, and the second from the Campanian to the Eocene. However, the curve is broadly similar to the exponential rises seen in other evolutionary expansions in which major taxonomic groups radiate into new adaptive zones of 'unoccupied ecospace' (Van Valen 1971; Stanley 1977; Sepkoski 1978). The rate of diversification flattens off, possibly when an equilibrium condition is reached at which the rate of origination of new taxa is balanced by extinction. The initial exponential rise need not necessarily mean that speciation rates are higher, alternatively, extinction rates may be lower (Rosenweig 1975).

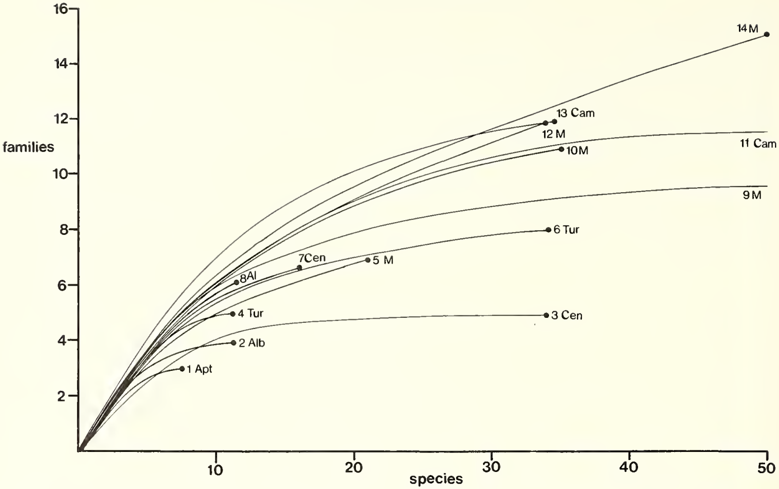
Rarefaction curves for species within families for individual Cretaceous faunas are shown in text fig. 10, these confirm the more or less progressive increase in diversity to the Maastrichtian stage. Rarefaction curves for most Cenozoic faunas and low-latitude Recent faunas are slightly higher than the Maastrichtian curves.



TEXT-FIG. 9. Diversity of species within families (H′) for Cretaceous faunas from the Aptian to the Recent. Bars show means, standard deviations and sample sizes. Data sources and other comments as for text-fig. 8.

Latitudinal distribution of fossil gastropods

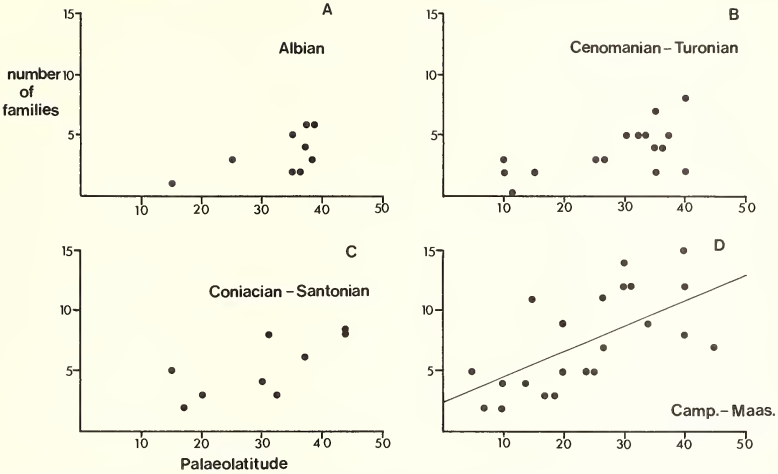
If the strong latitudinal gradient in species diversity seen in Recent predatory gastropod faunas, particularly as exhibited in the eastern Atlantic, existed in the past, then the patterns of increasing diversity through time may represent a response to environmental gradients. A low diversity recorded from a particular geological period may not represent a low global diversity but merely that all the faunas sampled came from a particular latitudinal range or similar environmental regimes. Thus in order to interpret correctly the changes of diversity with time it is necessary to examine the latitudinal distributions of gastropods at the particular time concerned.



TEXT-FIG. 10. Rarefaction curves (Raup 1975) of species in families for some of the most diverse Cretaceous faunas. Abbreviations represent Cretaceous stages. 1, Aptian, England (Morris and Cleevely, unpub.); 2, Loriol (1862); 3, Stephenson (1952); 4, Roman and Mazeran (1920); 5, Erikson (1974); 6, Stoliczka (1867-1868); 7, Geinitz (1874); 8, Blackdown Greensand (Morris and Cleevely, unpub.); 9, Stephenson (1941); 10, White (1888); 11, Sohl (1964*a*); 12, Stoliczka (1867-1868); 13, Sohl (1964*b*); 14, Kaunhowen (1898).

The latitudinal distribution of predatory families during various stages of the Upper Cretaceous is shown in text fig. 11. For the Albian, Cenomanian-Turonian, Coniacean-Santonian there are slightly more families at latitudes 30-40° N. and S. than at lower latitudes, although the number of families at all latitudes if fairly low. However, in Campanian-Maastrichtian times there is a pronounced diversity gradient with tropical faunas having less than half the number of species than faunas from higher latitudes. This gradient is of some interest, for it is, of course, in the opposite direction to that of the present day where most predatory families are found in tropical latitudes.

By the Eocene (text-figs. 12*b* and 13*b*), low-latitude predatory families were much more diverse, but although there is a slight gradient towards the poles this is not statistically significant. It is possible that if more well-collected and described low- and high-latitude faunas had been available this gradient may have been a little steeper. In the Miocene (text-figs. 12*a* and 13*a*) the predator diversity curve decreases polewards and is similar in form to the present-day gradient on the west coast of North America. Unfortunately, insufficient data points were available to separate Lower, Middle, and Upper Miocene faunas which may have illustrated the progressive effects of polar cooling in the late Miocene as evidenced from other sources (e.g. Addicott 1970*b*). Tropical diversities in the Miocene were about the same as at the present day, but European Miocene faunas were much richer in predatory gastropods than the equivalent eastern Atlantic latitudes today.



TEXT-FIG. 11*a–d*. Variation in the number of predatory gastropod families with palaeolatitude for various Upper Cretaceous stages. Lines are linear regressions. Data extracted from the following sources:

a. Albian: Allison (1955), Kollmann (1977, 1978), Loriol (1882), Mongin (1977), Morris and Cleevely (unpublished lists B.M. (N.H.)), Pervinquière (1912), Stanton (1947), Wollemann (1906).

b. Cenomanian–Turonian: Abbas (1963), Andert (1934), Archaic (1837), Blanckenhorn (1927), Chiplonkar and Badve (1972), Collignon (1934), Delpey (1940), Geinitz (1874), Hayami and Kase (1977), Parona (1909), Pchelintsef (1954), Pervinquière (1912), Roman and Mazeran (1920), Stephenson (1952), Stoliczka (1867–1868).

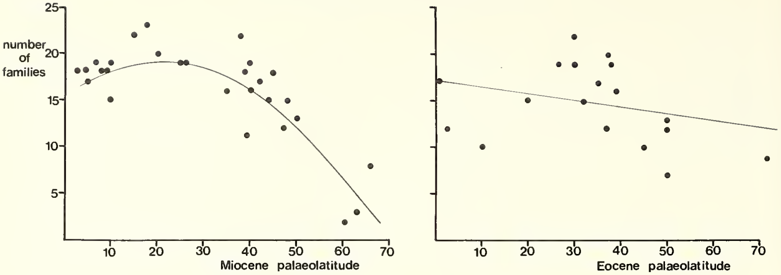
c. Coniacean–Santonian: Andert (1934), Blanckenhorn (1927), Böse (1923), Delpey (1938), Morris and Cleevely (unpublished), Nagao (1939), Pchelintsef (1954), Pervinquière (1912), Rennie (1945).

d. Campanian–Maastrichtian: Abbass (1963), Albanesi and Busson (1974), Collignon (1949, 1971), Douvillé (1904), Erikson (1974), Holzapfel (1888), Imlay (1937), Kaunhowen (1898), Krymgol'tz (1974), Morris and Cleevely (unpublished Rept. Ecuador), Myers (1968), Olsson (1934), Pervinquière (1912), Riedel (1932), Sohl (1964*a*, 1964*b*, 1967), Sohl and Mello (1970), Stephenson (1941), Stoliczka (1867–1868), White (1888).

Northern and southern hemisphere faunas plotted on the same 0–50° axis. Palaeolatitudes estimated from Smith and Briden (1977).

Compositional changes in fossil faunas

The Recent model shows that compositional changes occur with latitude, and such changes are also to be expected in fossil faunas as well as changes through geological time as a result of evolutionary replacement by more successful forms. In Cretaceous faunas from the Albian to the Campanian, the families Naticacea, Fasciolariidae, Volutidae, and Cancellariidae were generally the most diverse of the predatory taxa. Table 2 shows the percentage of various predatory families in various faunas of the Cenomanian-Turonian. Other families such as the Muricidae, Vasidae, and Melongenidae were diverse in some faunas. In the extra-tropical faunas of Campanian-Maastrichtian times, many more families such as the Turridae, Mitridae, Olividae, and Cymatiidae make an appearance (Table 3) but the most diverse families were clearly the Fasciolariidae and the Volutidae which form an average of

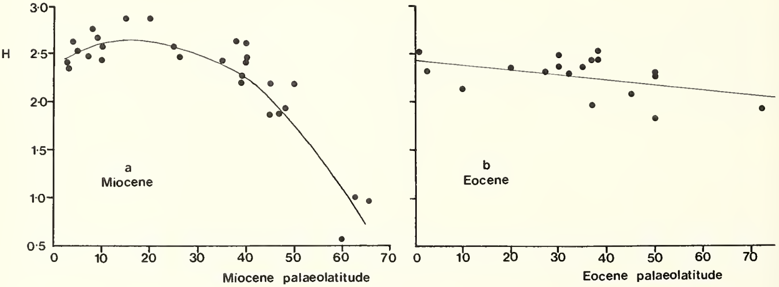


TEXT-FIG. 12*a–b*. Variation in the number of predatory gastropods with palaeolatitude for (*a*) Miocene faunas and (*b*) Eocene faunas. Curve in 12*a* is a five-point running mean, and line in 12*b* is a linear regression. Data extracted from:

a. Miocene faunas: Addicott (1970*a*), Beets (1941), Gardner (1936–1947), Glibert (1952*a*, *b*, Turridae from Peyrot, 1938), Hinsch (1977), Hornes (1851–1856), Ilona (1954), Ilyina (1963), Itojgawa *et al.* (1974), Iwasaki (1962), Jung (1965, 1969, 1971), Kanno (1971), Ludbrook (1973), Mansfield (1937), MacNeil (1973), Maury (1917), Nordsieck (1972), Olsson (1964), Pannekoek (1936), Perrilliat (1972–1973), Rasmussen (1968), Rutsch (1934), Sorgenfrei (1958), Strausz (1966), Uozumi (1962), Vredenburg (1925), Weaver (1942), Woodring (1957–1973).

b. Eocene faunas: Cossmann (1895–1898), Cossmann and Pissaro (1898–1901, 1911), Curry *et al.* (1968), Eames (1952, 1957), Glibert (1938), Iqbal (1972), Ludbrook (1973), Martin (1914, 1931), O'Gorman (1923), Olsson (1928), Ortmann (1902), Oyama *et al.* (1960), Palmer (1937, Turridae from Harris 1937), Vokes (1939), Weaver (1942), Zinsmeister and Camacho (in press).

Northern and southern hemisphere faunas plotted on the same 0–80° axis. Palaeolatitudes estimated from Smith and Briden (1977).



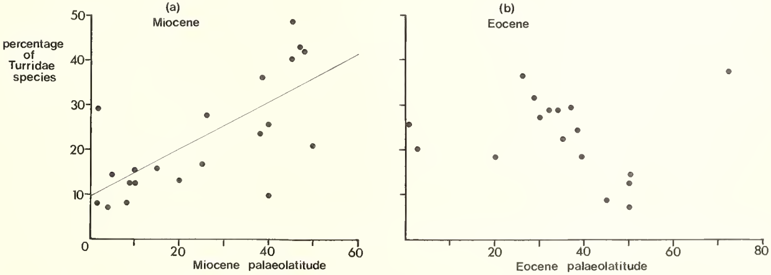
TEXT-FIG. 13*a–b*. Variation in the diversity of species within families (H′) with palaeolatitude for (*a*) Miocene and (*b*) Eocene faunas. Data as for text-fig. 12*a–b*. Curve in 13*a* is a five-point running mean, and line in 13*b* is a linear regression.

TABLE 2. Percentage of species in different predatory families in some Cenomanian–Turonian faunas.

	Woodbine Fm. Stephenson (1952)	Saxony Geinitz (1874)	S. India Stoliczka (1867–1868)	C. Asia Pchelinsef (1953)	Germany Andert (1934)
Naticacea	23·5	22·2	21·2	38·5	38·5
Cymatiidae		5·6	3·0		
Muricidae	5·9	16·7			
Buccinidae		22·2			
Melongenidae			12·1		
Fasciolariidae	11·8	5·6	12·1		23·0
Vasidae			12·1	3·8	15·4
Volutidae	38·2	5·6	30·3	50·0	15·4
Cancellariidae	20·6	22·2	3·0	3·8	7·7
Turridae			6·1		
Families	5	7	8	5	5
Species	34	18	33	26	13

20 and 13% of the predatory faunas respectively. The Fasciolariidae are particularly diverse in faunas from the south-eastern United States where they formed up to 25% of species. In tropical faunas of the Campanian-Maastrichtian, predators were neither diverse nor common, and Tethyan faunas typically contain a few species of Naticacea, Fasciolariidae, and Volutidae. The common naticid in these faunas is *Tylostoma*, a genus generally restricted to Tethyan faunas.

Sohl (1971) has documented the sharp compositional boundary between the tropical Cretaceous and sub-tropical temperate gastropod faunas that existed from Neocomian to Maastrichtian times in the Caribbean–North American area. A similar sharp faunal change existed between other Tethyan and higher-latitude faunas. The Tethyan faunas were characterized by abundant rudistid bivalves (Kauffman 1973) and acteonellid and nerineid gastropods. As discussed above, only relatively few predatory prosobranch gastropods occur in these faunas and these are relatively uncommon. Although changes did occur, these Tethyan faunas were extremely conservative and stable throughout the Upper Cretaceous, and it appears that most of the predatory prosobranch families first evolved at higher latitudes and not in the tropics as their present-day distributions would suggest.



TEXT-FIG. 14*a–b*. Variation in the percentage of Turridae species in the total predatory gastropod fauna with paleolatitude for (*a*) Miocene and (*b*) Eocene faunas. Data sources as for text-fig. 12*a–b*.

TABLE 3. Percentage of species in different predatory families in some Campanian–Maastrichtian faunas. Some minor families omitted.

	Ripley Fm. Sohl (1964*a*)	Coffee Sand Sohl (1964*b*)	Merchantville Fm. Sohl and Mello (1970)	Maastricht Kaunhowen (1898)	S. India Stoliczka (1867–1868)	Navarro Gp. Stephenson (1941)	Owl Creek Fm. Sohl (1964*a*)	NE. Brazil White (1888)	Aachen Holzapfel (1888)
Naticacea	7·3	11·8	19·0	22·0	32·3	11·3	6·3	37·1	
Cymatiidae	2·2			4·0	8·8				
Muricidae	8·0	6·9	9·5	2·0		5·2	4·8	8·6	3·2
Coraliophilidae	1·5	2·9					3·2		
Buccinidae	5·8	14·7	4·8	2·0	5·9	9·3	7·9	8·6	6·5
Melongenidae	8·8	5·9	4·8	2·0	5·9	2·1	6·3		6·5
Fasciolariidae	25·5	14·7	23·8	14·0	2·9	2·7	20·6	11·4	6·5
Vasidae	6·6	11·8	9·5	4·0	2·9	10·3	9·5		13·0
Olividae	3·6	2·9		2·0	2·9	1·0	7·9	2·9	
Volutidae	12·4	8·8	9·5	12·0	14·7	11·3	19·0	8·6	29·0
Mitridae		2·9		4·0	2·9				9·7
Cancellariidae	6·6	5·9	14·3	16·0	14·7	11·3	4·8	5·7	16·1
Turridae	10·2	11·8	4·8	10·0	2·9	15·5	7·9	5·7	
Families	14	12	9	15	12	10	12	10	8
Species	137	34	21	50	34	97	63	35	31

TABLE 3. Percentage of species in different predatory families in some Campanian–Maastrichtian faunas. Some minor families omitted.

	Ripley Fm. Sohl (1964*a*)	Coffee Sand Sohl (1964*b*)	Merchantville Fm. Sohl and Mello (1970)	Maastricht Kaunhowen (1898)	S. India Stoliczka (1867–1868)	Navarro Gp. Stephenson (1941)	Owl Creek Fm. Sohl (1964*a*)	NE. Brazil White (1888)	Aachen Holzapfel (1888)
Naticacea	7·3	11·8	19·0	22·0	32·3	11·3	6·3	37·1	
Cymatiidae	2·2			4·0	8·8				
Muricidae	8·0	6·9	9·5	2·0		5·2	4·8	8·6	3·2
Coraliophilidae	1·5	2·9					3·2		
Buccinidae	5·8	14·7	4·8	2·0	5·9	9·3	7·9	8·6	6·5
Melongenidae	8·8	5·9	4·8	2·0	5·9	2·1	6·3		6·5
Fasciolariidae	25·5	14·7	23·8	14·0	2·9	2·7	20·6	11·4	6·5
Vasidae	6·6	11·8	9·5	4·0	2·9	10·3	9·5		13·0
Olividae	3·6	2·9		2·0	2·9	1·0	7·9	2·9	
Volutidae	12·4	8·8	9·5	12·0	14·7	11·3	19·0	8·6	29·0
Mitridae		2·9		4·0	2·9				9·7
Cancellariidae	6·6	5·9	14·3	16·0	14·7	11·3	4·8	5·7	16·1
Turridae	10·2	11·8	4·8	10·0	2·9	15·5	7·9	5·7	
Families	14	12	9	15	12	10	12	10	8
Species	137	34	21	50	34	97	63	35	31

Both of the gastropod families, the Acteonellidae and the Nerineidae which dominate Tethyan tropical faunas are now considered to belong to the subclass Opisthobranchia. Most Nerineidae were probably infaunal gastropods inhabiting carbonate sands and muds. Although they have no obvious living relatives they may have been deposit feeders. On the other hand, although the relationships of the Acteonellidae with living shelled opisthobranchs are obscure, their morphology is generally similar. However, although most shelled opisthobranchs are predators, particularly upon other molluscs and polychaetes, some of the larger animals such as *Bulla*, *Hydatina*, and *Haminoea* are herbivorous (Thompson 1976). Thus there are no clear indications from comparisons with living forms whether acteonellids were herbivores or carnivores. Their great abundance in some deposits might suggest a herbivorous habit, but the light, buoyant shells of opisthobranchs often accumulate in post-mortem aggregations. If the Acteonellidae were predators, then it might be suggested that their abundance in tropical faunas during the late Cretaceous excluded the predatory prosobranch families which had apparently originated at higher latitudes. However, although the acteonellids are frequently abundant in Tethyan faunas they are not particularly diverse, and if morphological diversity gives some idea of a diversity of habits, then one would not expect a great variety of feeding types amongst them. By contrast, predatory prosobranchs exhibit such a diversity of food specializations, that exclusion by acteonellids was probably unlikely.

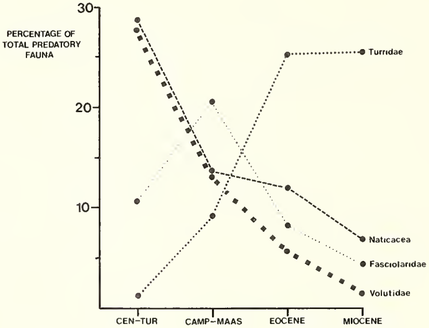
By the Eocene, the distribution patterns had changed considerably (Table 4), with the Turridae being the most diverse family in most samples and generally comprising some 25% of the species (text-fig. 15). The importance of the Turridae continued into the Miocene and in faunas from the European area up to 45% of species may be turrids. Families such as the Fasciolariidae and Volutidae which were diverse during the Cretaceous and formed a high proportion of the total predatory fauna were by the Eocene much less important and along with many other families formed only a relatively small proportion of the total predatory fauna. Although latitudinal gradients in faunal composition are not steep in the late Cretaceous and Eocene faunas, there are marked compositional changes in the Miocene. The Turridae are very important at higher latitudes, but at lower latitudes they comprise

TABLE 4. Mean percentage of species in different predatory families in faunas from the Cenomanian to the Miocene. Minor families omitted.

	Cenomanian–Turonian	Campanian–Maastrichtian	Eocene	Miocene
Naticacea	28·8	13·9	12·0	6·7
Cymatiidae	1·7	1·5	4·0	2·1
Ficidae			1·8	1·3
Cassididae			3·0	2·7
Muricidae	4·5	4·2	5·2	7·2
Columbellidae			1·2	3·9
Buccinidae	4·4	6·6	8·5	5·3
Nassariidae			1·9	6·9
Melongenidae	2·4	5·3	1·4	0·5
Fasciolariidae	10·5	20·5	8·1	4·4
Vasidae	6·3	9·6	0·3	0·5
Olividae		2·3	4·4	3·6
Volutidae	27·9	13·4	5·8	1·5
Marginellidae			3·4	1·8
Mitridae		2·9	3·9	5·0
Cancellariidae	11·5	7·8	3·8	5·6
Turridae	1·2	9·2	25·2	25·4
Conidae			3·6	6·3
Terebridae			1·0	5·2
No. of faunas sampled	5	10	10	17

only about 14% of the species; however, the two other toxoglossate families Conidae and Terebridae are more diverse at these lower latitudes. The Nassariidae, Fasciolariidae, and Cancellariidae also form a slightly greater proportion of the total predatory species at higher latitudes.

The importance of the Turridae has continued to the present day (text-fig. 5), especially in offshore and deep-sea sediments. The importance of the Buccinidae at high latitudes which is so pronounced in the present day, in all oceans, is a relatively recent occurrence from the late Miocene onwards and its development was not detected in this analysis; although some faunas from the late Miocene of northern Japan show an abundance of Buccinidae (Uozumi 1962; Chinzei 1978). The evolution of the important buccinid genus *Neptunea* in the northern Pacific has recently been documented by Nelson (1978) who shows how the group arose in the Miocene, spread around the northern Pacific, and then entered the Atlantic in the Plio-Pleistocene.



TEXT-FIG. 15. Changes in the relative proportions of various major families in the total predatory fauna from the Cenomanian–Turonian to the Miocene. Time axis not to scale.

Direct evidence of predation by fossil gastropods

Direct evidence of the activities of predatory gastropods in fossil faunas is afforded mainly by these predators which drill holes into shelled prey, that is, the Mesogastropod groups Naticacea and Cassididae and the Neogastropod family Muricidae. Another Mesogastropod family the Capulidae contains species which bore holes but these may be regarded as parasites (Matsukuma 1978). Predatory hole drilling is known in other molluscs particularly in the octopus (Wells 1978), the opisthobranch *Okadaia* (Young 1968), and in the predatory species of the terrestrial pulmonate gastropod family the Zonitidae (Mordan 1977). The last are true predators, other reports of shell boring in pulmonates seem to be instances of radulation for calcium carbonate.

The drilling activities of the Naticacea and Muricidae have been well documented, and Carriker and Yochelson (1968) suggest the criteria by which boreholes produced by gastropods should be recognized. There is an extensive literature concerning boreholes throughout the Cenozoic (e.g. Taylor 1970; Hoffman *et al.* 1974; Fischer 1966; Thomas 1976; Reyment 1966, 1967), and although boreholes have been attributed to gastropods throughout the Mesozoic and Palaeozoic, we agree with Carriker and Yochelson (1968) and Sohl (1969) that most pre-upper Cretaceous holes are equivocal in nature and generally uncommon.

The earliest unequivocal drillholes that we know of, and which occur in some abundance, are from the Albian Blackdown Greensand of south-west England, a little earlier than the Cenomanian records of Sohl (1969) and Fischer (1962, 1964); although borings attributed to gastropods have been recorded in some Aptian brachiopods of England (Laurie 1977). In the Blackdown Greensand both naticid and muricid drill holes occur in epifaunal and infaunal bivalves. The potential predators in the Blackdown Greensand include several naticid species and two or three species of muricid. Sohl (1969) observes that by the Campanian-Maastrichtian a wide variety of bivalves and gastropods were bored by predatory gastropods. Evidence of boring by Cassididae into the tests of echinoids is much less common, but examples are known from the Eocene (figured by Sohl 1969) and from the Oligocene (figured by Beu *et al.* 1972). Although the Naticacea have been in existence since at least the lower Jurassic, unambiguous naticid drill holes did not appear until the mid Cretaceous. Sohl (1969) correlates the beginning of the shell-drilling habit with the appearance of species of the subfamily Polynicinae; most naticaceans prior to the Albian belonged largely to the subfamily Ampullospirinae which were apparently not shell borers. In some Recent species such as *Polynices duplicatus* (Edwards 1975; Edwards and Huebner 1977) about 25% of the prey are not bored and it is possible that pre-Albian naticids may have eaten molluscan prey without hole drilling, but they would have been limited in the types of bivalve prey they could attack in this way.

The first appearance of convincing muricid drill holes corresponds quite well with the first appearance of muricid gastropods, and forms such as *Hillites*, *Sargana*, and *Rapana*-like forms are quite common in the lower part of the Upper Cretaceous. Some Recent species of Melongenidae, Fasciolariidae, and Buccinidae which wedge and chip at the valve margins of bivalve prey frequently suffer damage to the outer lip of the shell aperture. Nielsen (1975) illustrates the characteristic breakage and repair produced by these activities in *Buccinum undatum*, and these patterns should be recognizable in fossil gastropods.

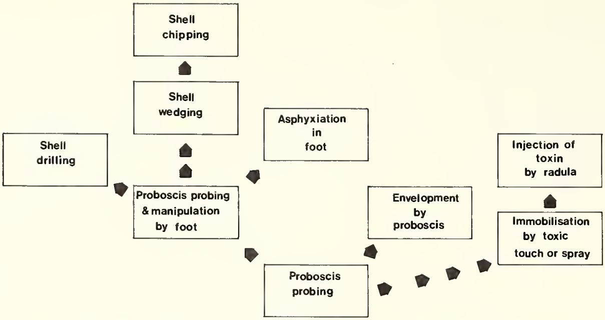
DISCUSSION AND CONCLUSIONS

Competition has been an important evolutionary force that has led to niche separation, specialization, and diversification (Pianka 1974). Empirical studies from living predatory gastropods strongly suggest that in the tropics at least, competitive interactions have been important in determining the habitat, occupation patterns, size and diets of gastropods at the specific level, and over a longer timespan at the familial level.

The rapid diversification and adaptive radiation of predatory families during the late Cretaceous may have arisen as a consequence of competitive interactions between taxa, giving rise to broad habitat separations and specializations upon particular food types. Selection will favour those phenotypes which maximize the energy extracted from particular food types, which results in anatomical and behavioural modifications to cope more efficiently with particular food types or habitats. The predators may have become canalized into particular prey or habitat types, and later diversification mainly occurred within these particular adaptive zones. For example, the specialized behaviour and anatomical modifications which enable the Cassididae to catch and eat echinoids are not very suitable for catching other prey types such as infaunal polychaetes. By contrast, some families have retained or acquired generalist feeding habits or habitat preferences which, as in the case of the Buccinidae, have resulted in diversification at high latitudes.

Amongst the earliest predatory gastropods are species from the families Fasciolariidae, Volutidae, Vasidae, Muricidae, Cymatiidae, and the superfamily Naticacea. These are families which today feed largely upon rather slow-moving or sedentary prey such as bivalves, gastropods, and sedentary polychaetes. The diet of the Cancellariidae, another family important in early faunas, is unknown. Of the three most diverse families in Albian to Campanian faunas the large Fasciolariidae use both the proboscis and the edge of the shell to gain entry into bivalve prey, whilst smaller species use only the proboscis to feed upon tube-living polychaetes (Paine 1966*a*). From what is known of the Volutidae, they feed upon gastropods and bivalves, and the Naticacea are well known for their shell drilling of molluscan prey.

Predatory taxa adept at catching more mobile prey were neither diverse nor abundant until the Campanian-Maastrichtian, when the Turridae became more important, but by the Eocene, this family of polychaete specialists is the most diverse in many faunas. Other specialist families such as the Cassididae, Tonnidae, Harpidae, Conidae, and Terebridae did not appear until the late Cretaceous or early Palaeocene. By comparison with living forms the feeding methods of gastropods became


Shell chipping
Shell wedging
Shell drilling
Asphyxiation in foot
Injection of toxin by radula
Proboscis probing & manipulation by foot
Envelopment by proboscis
Immobilisation by toxic touch or spray
Proboscis probing

TEXT-FIG. 16. Possible radiation of feeding behaviour in predatory prosobranch gastropods. See text for discussion.

more elaborate during the Upper Cretaceous. A possible radiation of gastropod feeding methods based upon observations of living animals is shown in Text-fig. 16. The co-evolution of predators and prey is important: as predators became more adept at catching and extracting prey, the prey species in turn evolved anti-predation devices and behaviour, such as the development of escape reactions, the selection of more cryptic habitats, shell thickening, and the elaboration of shell sculpture. Predatory gastropods probably developed from carnivorous forms feeding upon sedentary animals such as sponges and ascidians, as the Fissurellidae, Cypraeidae, Triphoridae, and Eratoidae do today. From this carnivorous habit the ability to feed upon slightly more mobile prey (sedentary polychaetes, other molluscs) developed. Initially predators may have developed better prey-seeking devices, with the elaboration of the osphradium and the anterior nervous system. The proboscis was developed for gaining access to the prey. Sedentary soft-bodied prey such as ptychoderid worms may be swallowed whole by the eversion of the proboscis. Free-living prey would have been held and manipulated by the foot and from this probably developed the feeding method employed by the Volutidae, Harpidae, and Olividae of holding and asphyxiating the prey in the foot, sometimes with the secretion of large quantities of mucus. An elaboration of the foot-grasping behaviour is the use of the outer shell lip of the gastropod to wedge between the valves of bivalve prey whilst the proboscis is inserted. In some groups this behaviour probably developed into the use of the shell lip for chipping the edges of bivalve prey.

Today zonitid pulmonate snails penetrate the shells of their snail prey by mechanical means only (Mordan 1977). Selection may have favoured those predators producing calciphagic enzymes, acids, and chelating agents from either the proboscis or the foot which allowed more efficient penetration of the shells. At first drill holes may have been concentrated at valve margins, a habit practised by some naticids today; but later, perhaps because of increased protection of the valve margins, and by the increased perfection of the drilling technique of the predators, the normal drill position moved towards the dorsal part of the shell, although this varies with prey and predator species. Similar drilling techniques also arose independently in the Cassididae. Prédatory gastropods which eat more active prey evolved the use of a toxic secretion, usually produced by modified oesophageal glands, to immobilize their prey after location. Some predators deliver the toxin by touch, as in *Thala*, a vexillid (Maes and Raeihle 1976) or squirt it as in some Cymatiidae (Houbrick and Fretter 1969), and in the toxoglossan families (Turridae, Terebridae, and Conidae) the radula teeth have become modified into hollow darts, down which the toxin flows after the prey has been impaled. The venom apparatus is not homologous in the families mentioned but they represent different ways of performing the task of delivering the venom and immobilizing the prey.

The main adaptive zones of predatory gastropods were probably established between Campanian and Eocene times. The constraints upon the width of the adaptive zone occupied by predatory prosobranch gastropods, other than anatomical or functional limitations, were and are probably the competitive effects of other predators of benthic invertebrates, notably opisthobranch gastropods, decapod crustacea, and teleost fish. Predation by other animals on predatory gastropods may have been limiting in certain environments. Although obviously new taxa have evolved during the Cenozoic, they have probably made little difference to the main adaptive zones of each family. For instance, the species of the genus *Drupa* of the Muricidae, which evolved fairly recently (Emerson and Cernohorsky 1973) feed upon similar prey to the Conidae and Mitridae, and occupy broadly similar habitats. Similarly, a small number of muricid species, notably in the genus *Drupella*, feed upon coral polyps, which are the dominant food of the family Coralliophilidae (Taylor 1976, 1978*a*), yet they represent small numbers of species when compared with those within the main adaptive zone of the Muricidae. More usually there have been massive diversifications within one broad feeding type or habitat as, for example, the several hundred extant species of polychaete feeding Conidae, the 550 genera of Turridae (Powell 1966), and the multitude of species of intertidal Muricidae.

A remarkable feature of the predatory prosobranch radiation is the approximately coeval appearance of the Tonnacea and the unrelated Neogastropod families, as well as a smaller, less spectacular radiation amongst the Naticacea. Many of the morphological adaptations of the Tonnacea parallel those within the Neogastropoda, and the shell-drilling habit arose independently and at approximately the same time within the Tonnacea, Naticacea, and Muricacea. The radiation of predators was not confined to gastropods, for as Vermeij (1977*a*) has pointed out, the late Mesozoic saw massive diversifications in predatory teleost fish (Greenwood *et al.* 1966) and crabs with crushing chelae (Vermeij 1977*b*). These, together with the major diversifications which occurred in non-predatory groups such as siphonate heterodont bivalves (Stanley 1977), echinoids (Kier 1974), and cheilostome Bryozoa (Schopf 1977) formed part of the major reorganization of marine communities which Vermeij (1977*a*) dubbed the 'Mesozoic marine revolution'. This contributed greatly to the steep increase in total diversity at the end of the Mesozoic documented by Valentine (1969, 1973) and the subject of much recent debate (Bambach 1977; Raup 1976; Sepkoski 1976; Signor 1978). The appearance of major groups of new predators armed with new techniques of hunting and catching prey had profound effects upon the structure and adaptations of benthic marine animals. The specializations of the predators are so diverse that probably no group of invertebrates would have escaped their effects. For instance, the rise in importance of siphonate bivalves documented by Stanley (1977) suggests that bivalves were effectively being 'driven underground' by the severe predation intensity on epifaunal and surface burrowers. Changes in gastropod shell morphology were probably also associated with increased predation pressure. In some communities today, such as the intertidal rocky shore, gastropods may be the dominant predators (Paine 1966; Menge 1978).

The most satisfactory explanation of the late Mesozoic diversification is the continental fragmentation-diversity model developed by Valentine and Mores (1970). As well as providing the isolation of faunas necessary for diversification, the development of north–south aligned continental margins resulted in an increase in the number of marine provinces from the relatively few of the Mesozoic to the chains of provinces along N.–S. continental margins as in the Cenozoic and Recent (Valentine, Foin, and Peart 1978). Additionally, Kauffman (1975) has stressed that the last extensive inundations of cratonic areas all over the world occurred during the Cretaceous. This flooding, which occurred as a series of major pulses, combined with the almost global development of warm-water marine climatic environments, provided vast new areas for the proliferation and dispersal of marine animals. The development of new shallow-water habitats coupled with the isolating effects of continental fragmentation probably encouraged rapid diversification of unrelated groups of marine animals.

The numerous latitudinal faunal boundaries of the Cenozoic and Recent, formed by temperature discontinuities, may be unique in the Phanerozoic record, and the latitudinal thermal gradient in the Mesozoic was apparently lower and more gentle compared with the Neogene and Recent. Addicott

(1970*b*), for instance, documents the increase in provinciality of west American molluscan faunas throughout the Cenozoic with the late Miocene cooling producing the greatest provinciality of faunas. This increasing provinciality produced the diversifications of predatory gastropods seen during the Cenozoic, but generally within adaptive zones established during the Late Cretaceous and early Paleogene. Nevertheless, the adaptive radiation of predatory prosobranch gastropods is one of the more remarkable diversifications in the evolutionary history of the Mollusca and the invertebrates.

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THE ORNITHISCHIAN DINOSAUR *CAMPTOSAURUS PRESTWICHII* FROM THE UPPER JURASSIC OF ENGLAND

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ABSTRACT. The holotype of *Iguanodon prestwichii* Hulke, a reasonably complete skeleton from the Lower Kimmeridge Clay (Upper Jurassic, Lower Kimmeridgian) near Oxford, is redescribed and, because it is very similar to that of *Camptosaurus dispar* from the Upper Kimmeridgian of North America, is referred to the genus *Camptosaurus* as *C. prestwichii* (Hulke). The skeleton of *C. prestwichii* is more gracile and differs in a few other respects from those of *C. dispar*. *C. prestwichii* is the only undoubted species of *Camptosaurus* described from outside North America. The intramaxillary cavity of *Camptosaurus* probably housed a gland. Only the base of the paroccipital process of *C. prestwichii* is formed by the opisthotic, with the exoccipital forming the main occipital part. Documentation of an English species of *Camptosaurus* provides evidence for a land connection between Europe and North America some time during the early Late Jurassic, but the hypsilophodontid *Dryosaurus* may have used a different route between East Africa and North America.

PRESTWICH in 1879 announced the discovery of a skeleton of a new species of *Iguanodon* from the Lower Kimmeridge Clay (Upper Jurassic) at Cumnor Hurst near Oxford. The locality is Chawley Brick Pit, Hurst Hill, Cumnor, 2·5 miles west-south-west of the centre of Oxford (National Grid Reference SP 475 043). Prestwich (1880) provided a more detailed account of the geological occurrence of the specimen, which was named *Iguanodon prestwichii* by Hulke (1880, species name incorrectly given as *prestwichi* by most subsequent authors). The only description available of this reasonably complete skeleton is that given by Hulke (1880) who described most of the bones but only figured a few pieces of the skull, some teeth, the sacral centra, eight other vertebrae, and the proximal tarsals. Seeley (in Hulke 1880) considered that *I. prestwichii* represented a new genus, for which he subsequently (1888) erected the name *Cumnoria*. Lydekker (1888*a*) questioned the validity of the new genus and catalogued (1888*b*) the species as *I. prestwichii*. Lydekker (1889, 1890*a*) subsequently referred the species to the genus *Camptosaurus* Marsh (1885) as *Camptosaurus prestwichii* (Hulke). Gilmore (1909) redescribed the material of *Camptosaurus* from the Upper Jurassic of western North America and, after reviewing the description given by Hulke (1880), accepted *C. prestwichii* as a valid species of *Camptosaurus*.

In the intervening seventy years, *C.* (*Cumnoria*) *prestwichii* has received only a few passing mentions, with no restudy of the holotype. Consequently, almost a century later, the description given by Hulke (1880) still provides the only information available on this specimen. The specimen from the Lower Kimmeridge Clay (upper Lower Kimmeridgian, *Aulacostephanus pseudomutabilis* Zone, *c.* 141 m.y. ago, Van Hinte 1976) is important because it is a reasonably complete skeleton of an ornithopod dinosaur, a rare occurrence in the Middle and Upper Jurassic. Excellent material of ornithopod dinosaurs is known from the Morrison Formation (Upper Jurassic, Upper Kimmeridgian ≡ Lower Tithonian) of western North America (*C. dispar*, see p. 412), hypsilophodontids *Dryosaurus altus*, *Othnielia* Galton, 1977*a* (see Galton and Jensen 1973 as *Nanosaurus ?rex*)) and the Tendaguru Beds (Upper Kimmeridgian) of Tanzania (*D.* (= *Dysalotosaurus*) *lettowvorbecki* see Galton 1977*a*, *b*). A partial skeleton from the Upper Jurassic of Szechuan, China, was described as the iguanodontid *Sanpasaurus yaoi* Young (1944) but Rhozhdestvenskii (1967) showed that most of this material is that of a small sauropod dinosaur. The few other remains of ornithopod dinosaurs from the Middle and Upper Jurassic consist of single isolated bones (Steel 1969). Consequently, the material from Cumnor

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is the only associated skeleton of a non-hypsilophodontid dinosaur described from the Middle or Upper Jurassic outside North America. *Camptosaurus* is one of the few dinosaurian genera cited (Charig 1973; Galton 1977*b*) as occurring in the Upper Jurassic on both sides of the North Atlantic. If the Cumnor species is correctly referred to *Camptosaurus*, then the intercontinental distribution of this genus required the presence of a land route between western North America and southern England in the early part of the Late Jurassic.

Examination of the holotype of *I. prestwichii* resulted in the identification of all important pieces of bone apart from isolated pieces of neural arches and ribs. A redescription is needed for several reasons: Hulke (1880) provided an excellent description of the skull roof, braincase, jaws, and teeth, but additional cranial elements are now recognized, several of the bone identifications in the original description (one of the earliest for most of the bones of an ornithopod skeleton) are now found to be incorrect, and most of the bones of this skeleton have never been figured.

Unless noted to the contrary, the following references were used for comparative data on frequently cited ornithopod genera: Upper Jurassic, North America, *Camptosaurus* (Gilmore 1909), hypsilophodontid *Othnielia* Galton, 1977*a* (Galton and Jensen 1973 as *Nanosaurus ?rex*); East Africa, hypsilophodontid *Dryosaurus* (Janensch 1955); Lower Cretaceous, Europe, hypsilophodontid *Hypsilophodon* (Galton 1974*a*), iguanodontids *Ouranosaurus* (Taquet 1976), and *Iguanodon* (Hooley 1925); North America, *Tenontosaurus* (Ostrom 1970); Upper Cretaceous, North America, hypsilophodontid *Parksosaurus* (Parks 1926 as *Thescelosaurus warreni*), thescelosaurid *Thescelosaurus* (Gilmore 1915).

The reasons for referring *I. prestwichii* Hulke (1880) to the genus *Camptosaurus* rather than to the separate genus *Cumnoria* Seeley (1888) are discussed below (p. 431). In the comparative section, many references are made to the Morrison material of *Camptosaurus* Marsh (1885), five species of which were recognized by Gilmore (1909). Later, Gilmore (1925) recognized three species, the genotype *C. dispar*, the small *C. nanus*, and the large *C. amplus*. Gilmore (1925) noted that *C. medius* is perhaps a female *C. dispar*, and *C. browni* is probably a fully grown *C. medius*. Janensch (1955) noted that the characters used to distinguish *C. nanus* from *C. dispar* were probably juvenile features. The holotype of *C. amplus* is a pes of the carnivorous theropod *Allosaurus fragilis* (Bakker, pers. comm.; Gilmore 1909, pl. 17, cf. fig. 35, and Madsen 1976, pl. 53). The holotypes of four species of *Camptosaurus* (*C. dispar*, *medius*, *nanus*, *browni*) all came from Quarry 13 near Como, Wyoming (see Ostrom and McIntosh 1966; Gilmore 1909), and, given the range of individual variation shown by two species of *Dryosaurus* (Galton 1977*a*, *b*) and by *Hypsilophodon foxii*, it is reasonable to refer all the Morrison material to one species of *Camptosaurus*, *C. dispar* (Marsh 1879), and references to *Camptosaurus* given in the comparative section are to this American species.

Institution names have been abbreviated as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; CUM, Cambridge University Sedgwick Museum; HMN, Humboldt Museum for Naturkunde, East Berlin; OUM, University Museum, Oxford; USNM, United States National Museum, Washington DC; YPM, Peabody Museum, Yale University, New Haven.

DESCRIPTION AND COMPARISONS OF *CAMPTOSAURUS PRESTWICHII* (HULKE)

(based on specimen no. J330 in the University Museum, Oxford)

Skull

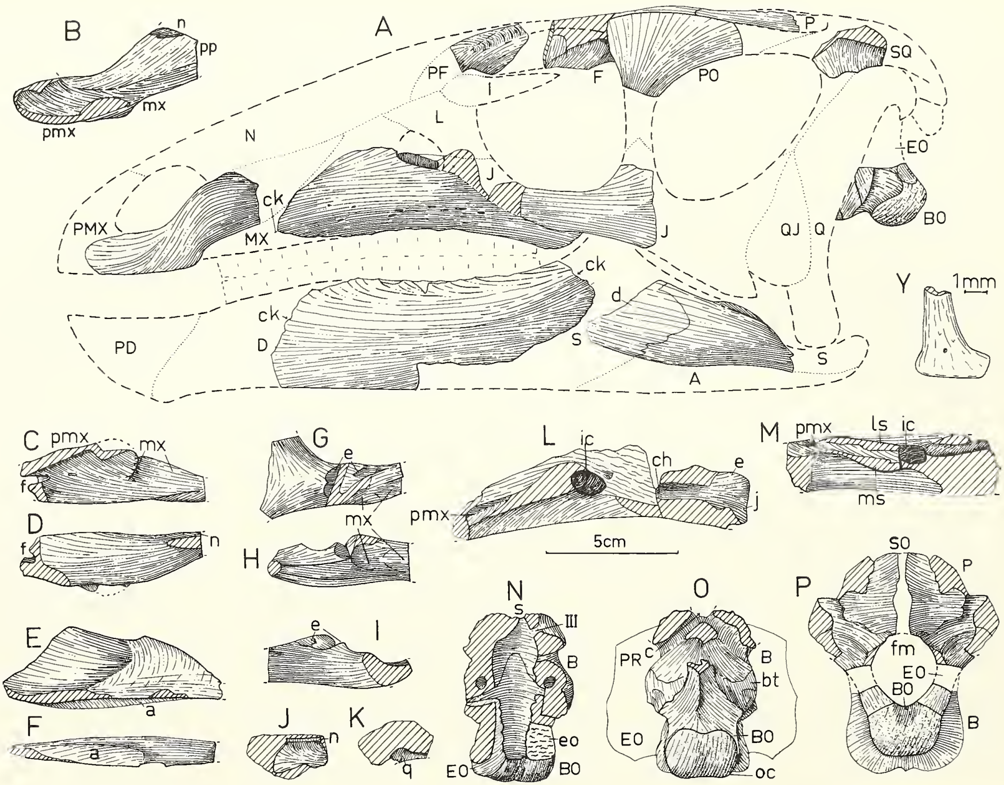
Apart from the braincase (text-fig. 1N-R; pl. 51, figs. 1-4), all the bones of the skull have separated at the sutures, and this presumably indicates that the animal was not an adult. The skull is long and low but broad (text-fig. 1A, S) rather than being proportionally higher and narrower as in all other ornithopod dinosaurus with the exception of *Camptosaurus*, *Ouranosaurus*, and some hadrosaurs (e.g. *Anatosaurus*, Lull and Wright 1942). However, the form of the individual bones is similar only to those of *Camptosaurus* (text-figs. 1A, 2A, B).

Dermal bones. The premaxilla (text-fig. 1A–D; pl. 52, fig. 16) is edentulous, and anteriorly there is a prominent foramen on the ventral surface (text-fig. 1D). This foramen appears to have opened on the lateral surface at the base of the anterior process, as does a comparable foramen in the premaxilla of *Camptosaurus* (Gilmore 1909, fig. 6). The massive posterior process overlapped the nasal dorsally (text-fig. 1A, B) and the maxilla fitted against its ventral surface, which has prominent sutural ridges at its base (text-fig. 1B, C; pl. 52, fig. 16). As in *Camptosaurus* (YPM 1880) and *Dryosaurus* (HMN dy 14), there is an anteriorly tapering groove on the medial surface (text-fig. 1B; pl. 52, fig. 16) which received a medial process of the maxilla and, as a result, the anterior end of the maxilla was probably expanded transversely, with an anteriorly projecting medial process as in *Camptosaurus* (YPM 1886), *Dryosaurus* (Janensch 1955, p. 11, fig. 2; YPM 1876), and the ornithopod *Priodontognathus* (CUM B53408, left maxilla, see Seeley 1875*a*, pl. 20, figs. 1, 2 for internal and external views). The posterior process of the premaxilla fitted into a groove on the antero-dorsal edge of the maxilla (text-fig. 1L, M; pl. 51, figs. 13, 14) as in *Camptosaurus* (USNM 5819; YPM 1886), *Dryosaurus*, *Iguanodon*, and *Ouranosaurus*. The antero-dorsal part of the maxilla is transversely constricted; dorsally, only the bases of the two sheets against which the anterior part of the lachrymal fitted are preserved. There is a well-defined sutural surface for the ectopterygoid on the jugal (text-fig. 1G, I; pl. 52, fig. 15) and, as the jugal is narrower than the maxilla (text-fig. 1I, L), the ectopterygoid also fitted against the postero-dorsal part of the maxilla.

About 15 mm above the maxillary tooth row, there is a prominent horizontal ridge with fine striations on the lateral surface (text-fig. 1A; pl. 52, fig. 7) which probably represents an attachment area for a muscle functionally analogous to the cheeks of mammals (Galton 1973*a*). Anteriorly, and also below this ridge, the lateral surface is pierced by several small foramina which pass obliquely backward. The foramina presumably unite within the maxilla and emerge postero-dorsally through a deep channel medial to the sutural area for the jugal (text-fig. 1L; pl. 52, fig. 14). Most of the maxilla is solid bone with a small fossa (text-fig. 1L, M; pl. 52, figs. 13, 14) immediately below the external antorbital fenestra (text-fig. 1A). The fossa opens dorsally and, in the left maxilla, this uncrushed oval aperture is 14 mm long and 10 mm wide, while the fossa is 11 mm deep with the walls progressively tapering inwards. In *Camptosaurus* (YPM 1886; Gilmore 1909, fig. 7) the fossa or intramaxillary cavity is proportionally much longer, extending a distance equal to a little more than four crown-widths posteriorly from the anterior border of the external antorbital fenestra, with the floor slightly above the most ventral line of the lateral foramina. Examination of several maxillae (USNM 5819; YPM 1886, 7417) indicates that these foramina do not pass into the intramaxillary cavity, and presumably they eventually pass into the postero-dorsal channel. Posteriorly the cavity appears to be completely closed off from the postero-dorsal channel by a narrow transverse bar of bone. Although the intramaxillary cavity of *Camptosaurus* is proportionally much larger, it also opens only dorsally.

The intramaxillary cavity is a remnant of the antorbital fenestra of thecodontians, which became enclosed by the maxilla. The large antorbital fenestra of thecodontians (Walker 1961; Ewer 1964) and the large intramaxillary cavity of lower ornithischians (Galton 1974*a*) probably acted as the area of origin of an anterior component of the pterygoideus musculature. However, Ewer (1964) notes that the original function of a small antorbital fenestra of thecodontians was probably to house a gland that might have been a nasal salt gland. The pit-like form of the intramaxillary cavity (text-fig. 1C) clearly precludes any function as an area of muscular attachment, and this also appears to be the case in *Camptosaurus*. The only structure which could have occupied such a cavity is a gland. The large antorbital fenestra and intramaxillary cavity of the ornithischian dinosaur *Hypsilophodon* may have provided an area of origin for an anterior component of the pterygoideus musculature (Galton 1974*a*) and, in addition, a gland probably occupied part of the cavity.

The upper orbital margin is formed principally by the prefrontal and postorbital, parts of which are rugose, with only a small contribution from the frontal (text-fig. 1A, T, S; pl. 51, figs. 5, 6). The orbital part of the postorbital (text-fig. 1A, S) is similar to that of *Camptosaurus* (USNM 5473; Gilmore 1909, pl. 10; USNM 7421) and the continually smooth curve shown for the postero-dorsal part of the orbit (text-fig. 2A; Gilmore 1909, fig. 3) is inaccurate. A groove on the medial edge of the prefrontal probably fitted against the nasal (text-fig. 1J, T, S), and the posterior end fitted into the frontal (text-fig. 1A, T, U, W). The medial surface of the posterior process of the postorbital has a triangular sutural area (text-fig. 1T; pl. 51, fig. 6) for the squamosal, only a small part of which is preserved (text-fig. 1A, K). The postorbital and frontal have a broad and complex sutural surface (text-fig. 1S, T, X; pl. 51, figs. 5, 6), the details of which are the same as in *Camptosaurus* (USNM 7421), and both bones are overlapped by the parietal postero-laterally (text-fig. 1S, T). The skull roof (text-fig. 1S) is similar to that of *Camptosaurus* (Gilmore 1909, pl. 10). The postorbital and frontal together form a sutural surface for the expanded anterior end of the laterosphenoid (as in *Camptosaurus* USNM 5473 and *Hypsilophodon*), with the rest of the bone fitting against the parietal (text-fig. 1T; pl. 51, fig. 6).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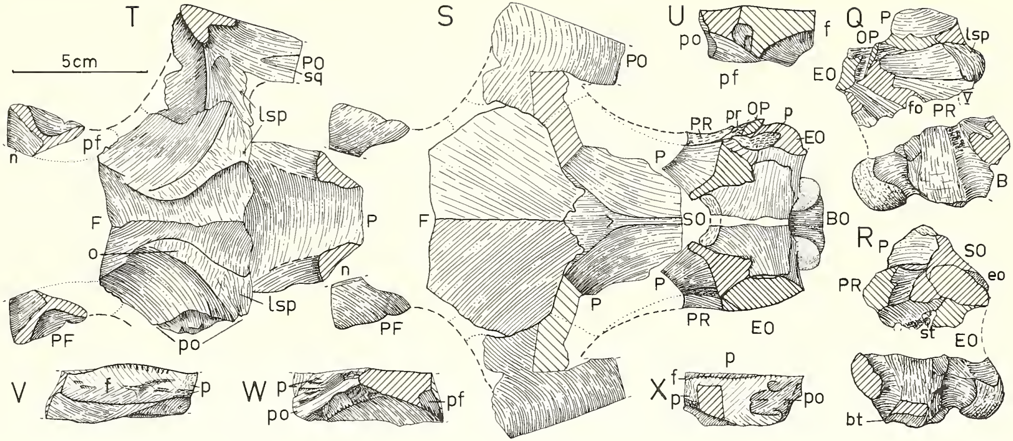


TEXT-FIG. 1. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. Skull bones. A, reconstruction of skull in left lateral view with bones arranged in an appropriately distorted outline of the skull of *C. dispar* (after Gilmore 1909); B–D, right premaxilla in B, medial (see pl. 52, fig. 16); C, ventral and D, dorsal views; E, F, right surangular in E, medial and F, ventral views; G–I, left jugal in G, medial (see pl. 52, fig. 15); H, ventral and I, dorsal views; J, left prefrontal in medial view; K, right squamosal in medial view; L, M, maxillae in dorsal view, L, left (see pl. 52, fig. 14), M, right (see pl. 52, fig. 13); N–R, braincase, N, dorsal view of floor (see pl. 51, fig. 4), O, ventral view (see pl. 51, fig. 3); P, posterior view; Q, outline of right lateral view, compare with pl. 51, fig. 1; R, outline of left lateral view; S, dorsal view of posterior skull roof and braincase (see pl. 51, figs. 2, 5); T, ventral view of posterior skull roof (see pl. 51, fig. 6); U–X, right frontal in U, anterior; V, medial; W, lateral and X, posterior views; Y, stapes (×4). For T, S, P, O, and N see also Hulke (1880, pl. 18, figs. 1–5). In all figures broken bone is indicated by mechanical shading. Abbreviations: A, angular; B, basisphenoid; BO, basioccipital; D, dentary; EO, exoccipital; F, frontal; I, infraorbital (= supraorbital); J, jugal; L, lachrymal; MX, maxilla; N, nasal; OP, opisthotic; PO, postorbital; PR, prootic; Q, quadrate; QJ, quadratojugal; S, surangular; SQ, squamosal; SO, supraoccipital. The same abbreviation in lower case indicates a sutural surface for that bone on another bone. bt, basisphenoid tubera; c, route of internal carotid artery; ch, channel; ck, ridges for attachment of cheeks; e, surface for ectopterygoid; f, combined foramen lacerum posterius and jugular foramen for internal jugular vein; fm, foramen magnum; fo, fenestra ovalis; ic, intramaxillary cavity; ls, lateral sheet; ms, medial sheet; o, surface for orbitosphenoid; oc, occipital condyle; pp, posterior process; s, sella turcica or pituitary fossa; st, stapes. III, oculomotor foramen; V, trigeminal nerve.

Braincase. A detailed description of the braincase (text-fig. 1Q, R, S; pl. 51, figs. 1-4) was given by Hulke (1880). The postero-lateral parts of the parietal fit closely on each side of the supraoccipital (text-fig. 1P, S; pl. 51, fig. 2) which is proportionately larger than it is in *Camptosaurus* (USNM 5473). As also in *Camptosaurus*, *Dryosaurus*, and *Hypsilophodon*, the supraoccipital is not excluded from the dorsal margin of the foramen magnum, as it is in *Iguanodon* (Dollo 1883*a*). The following features occur also in *Camptosaurus*: the postero-dorsal surface of the exoccipital lateral to the foramen magnum bears a prominent subcircular depression; ventrally the exoccipitals contribute to the lateral part of the occipital condyle (text-fig. 1P); and anterior tongue-like process of the basioccipital fits into a corresponding notch in the basisphenoid (text-fig. 1N, O; pl. 51, figs. 3, 4), and ventrally the process has a sharp median crest that arises out of a depression immediately anterior to the occipital condyle (text-fig. 1O). The flared-out antero-lateral part of the basioccipital is embraced by the massive buttress-like basisphenoid tubera (text-fig. 1O; pl. 51, fig. 3). Anteriorly the floor of the braincase has broken at the level of the posterior part of the sella turcica (text-fig. 1N, O) and more ventrally along the postero-laterally directed canals through which the internal carotid arteries passed to the pituitary fossa. Only the dorsal parts of these canals are preserved, and dorso-laterally it merges with the groove in which rami of the trigeminal and facial nerves passed ventrally after exiting from the braincase (text-fig. 1Q, R; pl. 51, fig. 1; see also Galton 1974*a*).

In nearly all ornithischians including *Camptosaurus* there is no trace of the suture between the exoccipital and the opisthotic, so the composition of the paroccipital process cannot be determined. This is the case on the left side (text-fig. 1R, S), but on the right the opisthotic is represented by a separate element which overlaps the antero-lateral part of the base of the paroccipital process and which is itself overlapped by the tapering dorsal part of the prootic (text-fig. 1Q, S; pl. 51, fig. 1). More ventrally the bone is broken, but the arrangement resembles that of the braincase of a juvenile hadrosaur described by Langston (1960) in which the main occipital part of the paroccipital process is formed by the exoccipital. In *Hypsilophodon*, the only other ornithischian for which information is available, the exoccipital is restricted to the lateral part of the occipital condyle. Anteriorly the prootic abutted against the dorsal part of the laterosphenoid and was itself slightly overlapped more ventrally (text-fig. 1Q; pl. 51, fig. 1). Breaks go through all of the cranial foramina, and the ventral borders of a few are preserved (text-fig. 1Q, R; pl. 51, figs. 1, 4). The dorsal part of the large foramen at the junction of the prootic and opisthotic is separated by a thin vertical septum. This area is similar to that of *Camptosaurus* and *Hypsilophodon* in which the anterior part is interpreted as the fenestra ovalis and the posterior and ventral parts as a combined foramen lacerum posterius and jugular foramen (Galton 1974*a*).

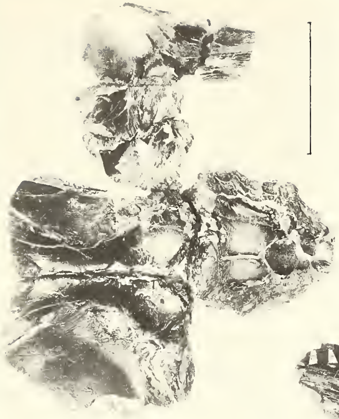
Mandible. The lateral surface of the dentary has a well-defined horizontal ridge (text-fig. 1A) which probably served as an attachment area for the cheeks (Galton 1973*a*). The medial view of the dentary (pl. 52, fig. 17) resembles that of *Camptosaurus* (Gilmore 1909, fig. 8), including the presence of a sutural area below the posterior six teeth which was probably for the antero-ventral part of the coronoid bone. The surangular (text-fig. 1A, E, F) is a sheet-like bone that was presumably overlapped antero-laterally by the dentary, which thickens ventrally to form a ventral surface, bordered laterally by a distinct edge, against which the angular fitted. A bevelled edge on the postero-lateral edge probably represents the posterior part of the insertion area of the M. adductor externus superficialis (see Ostrom 1961; Galton 1974*a*).

Dentition. The premaxilla is edentulous. The left maxilla has thirteen teeth and the left dentary has fourteen teeth, with two or three probably missing in each case, to give the same total count as for *C. dispar* (fourteen and fifteen or sixteen). Most of the teeth are broken, and only the crowns of incompletely erupted teeth are preserved. The original appearance of the dentary tooth row must have been as in *Camptosaurus* (Gilmore 1908, fig. 8). Several of the roots of functional teeth of the dentary show evidence of resorption adjacent to, and slightly above, the crown of the replacement teeth (pl. 52, fig. 7). In a study of tooth replacement in reptiles, Edmund (1960) found that all the teeth with 'odd' numbers in a numbered tooth series are replaced in sequence, followed by the 'even'

EXPLANATION OF PLATE 51

Cranial bones of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303.

Fig. 1, braincase in right lateral view (cf. text-fig. 1Q), $\times\frac{2}{3}$.
Fig. 2, braincase in dorsal view (cf. text-fig. 1S), $\times\frac{2}{3}$.
Fig. 3, floor of braincase in ventral view (cf. text-fig. 1O), $\times\frac{2}{3}$.
Fig. 4, floor of braincase in dorsal view (cf. text-fig. 1N), $\times\frac{2}{3}$.
Fig. 5, frontals and parietals in dorsal view (cf. text-fig. 1S), $\times\frac{1}{2}$.
Fig. 6, frontals, parietal and left postorbital in ventral view (cf. text-fig. 1T), $\times\frac{1}{2}$.
Fig. 7, damaged right maxilla in lateral view (cf. text-fig. 1A), $\times\frac{1}{2}$.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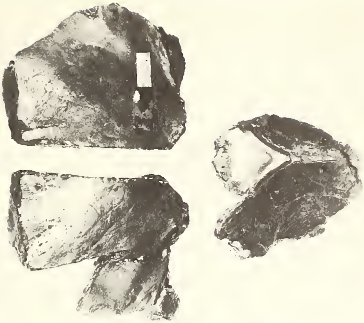
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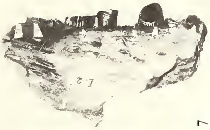
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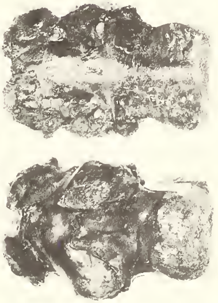
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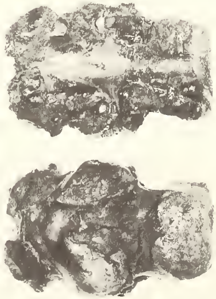
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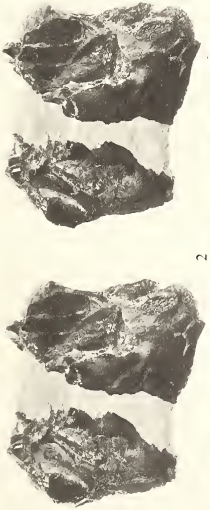
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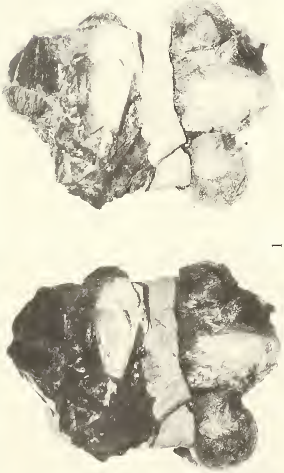
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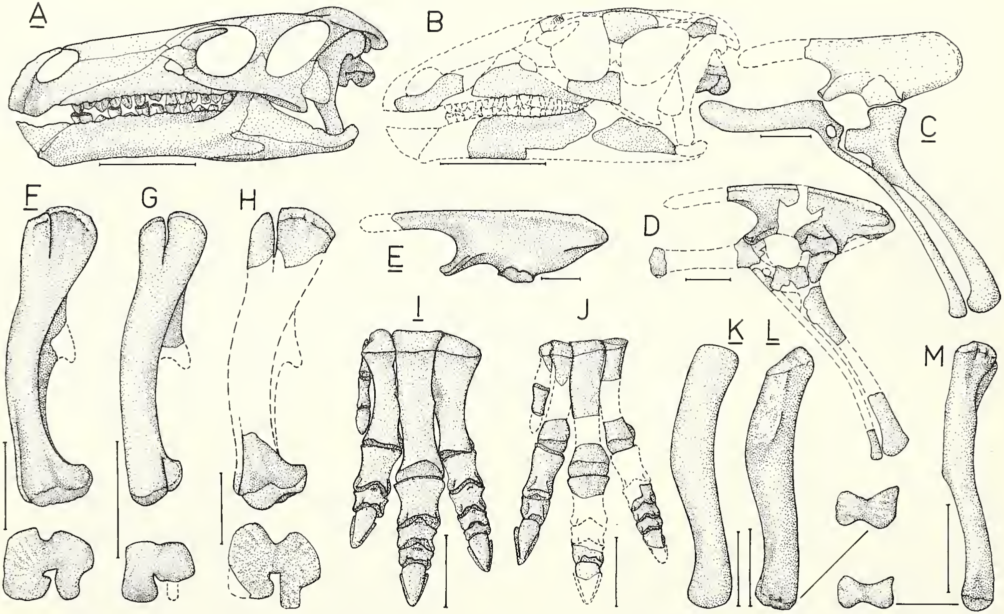
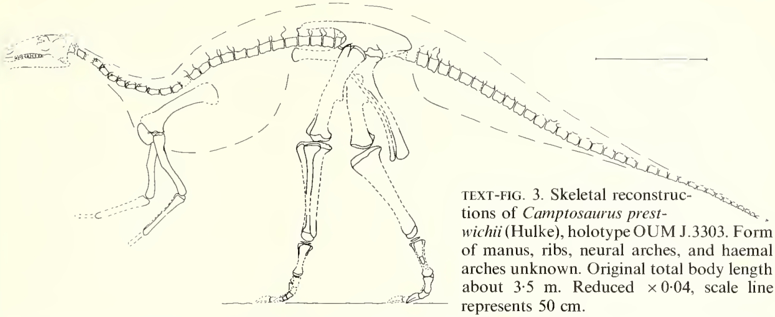
GALTON and POWELL, dinosaur *Camptosaurus*



TEXT-FIG. 2. Comparison of *Camptosaurus dispar* (A, C, E, F, I, K, L; identifying letters underlined to facilitate comparisons) from Upper Jurassic of North America with *C. prestwichii* (OUM J.3303, B, D, H, J, M) from Upper Jurassic of England and '*C.*' *leedsi* (G, holotype BMNH R1993) from Middle Jurassic of England. A, B, skull; C, D, pelvic girdle; E, ilium; F–H, femur; I, J, pes; K–M, humerus. Views—left lateral (A–H, K–M), dorsal or anterior (I, J) and with distal end included (F–H, L, M). A, C, E after Gilmore (1909), K after Gilmore (1912), F, I, L holotype YPM 1877. Scale line represents 10 cm.



TEXT-FIG. 3. Skeletal reconstructions of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. Form of manus, ribs, neural arches, and haemal arches unknown. Original total body length about 3·5 m. Reduced ×0·04, scale line represents 50 cm.

and, in most cases, the waves of tooth replacement pass anteriorly, so that the replacement teeth of each series become progressively smaller passing anteriorly. This pattern is clearly seen in the right maxilla and in both dentaries (pl. 52, fig. 7; Hulke 1880, pl. 18, fig. 8) as is also the case in *Camptosaurus* (Gilmore 1909, fig. 8). In *Hypsilophodon* and other lower ornithopods (Galton 1973*b*), there is a shallow groove bearing a line of foramina, one per tooth position, for the access of replacement teeth (Edmund 1957), on the medial surface above the maxillary tooth row and below the dentary tooth row. Although these foramina are absent in the material figured by Gilmore (1909), this is probably due to damage, as they are well shown by other specimens (YPM 1886, 1889, 7416, 7417, 7419, 7421).

The teeth were well described by Hulke (1880) and are very similar to those of *Camptosaurus* (pl. 52, figs. 1–12). The crowns are roughly lozenge-shaped and the antero-posterior width is greater for dentary teeth than it is for maxillary teeth, whereas the reverse is true for the transverse thickness. The shiny enamelled surface of the elaborately sculptured side of the crown (lateral for maxilla, medial for dentary) merges smoothly into the matt surface of the root with a sinuous line as the only sign of the cingulum (pl. 52, figs. 3, 4, 7). On the plain side of the crown, only the denticulate half of the crown height is covered with a thin layer of enamel, which shows a few faint transverse ridges, and a few of the terminal denticles are prolonged into short ridges (pl. 52, fig. 1). The sides of the non-denticulate half of the crown of maxillary teeth show only a small degree of convergence toward the root, whereas in dentary teeth it is much more marked (pl. 52, figs. 3, 7–9). On maxillary teeth, the anterior and posterior edges of this half of the crown form distinct ridges, whereas only the posterior edge of dentary teeth forms such a ridge (pl. 52, figs. 3, 7–9). In dentary teeth, the medial surface of the upper end of this ridge has a series of extremely fine serrations (6 in 2 mm; pl. 52, figs. 7–9). Traces of these serrations are visible on the anterior ridge of a maxillary tooth and also in the corresponding positions on very well-preserved dentary and maxillary teeth of *Camptosaurus* (USNM 5819; YPM 7416) and *Iguanodon* (Owen 1861*a*).

The prominent vertical keel on the lateral surface of the maxillary teeth is proportionally closer to the posterior edge than it is in most specimens of *Camptosaurus* other than USNM 5818 (pl. 52, figs. 2, 3, 6). On the medial surface of dentary teeth this ridge is smaller and it is just posterior to the centre of the crown, as it is in *Camptosaurus* (pl. 52, figs. 7–12). There are no secondary vertical ridges posterior to this keel in maxillary and dentary teeth (pl. 52, figs. 2, 3, 7–9). This is also the case for some teeth of *Camptosaurus* (dentaries USNM 4281; YPM 1886, pl. 52, fig. 10) and in other teeth (pl. 52, figs. 6, 11, 12) the number of ridges in this position varies from one to four. Anterior to the prominent keel there are several ridges of different lengths (pl. 52, figs. 2, 3, 7–9). For maxillary and dentary teeth, the number of ridges reaching the base of the crown is 3 and 2 respectively (in *Camptosaurus* the numbers are 2, 3 or 4, and 2), the number reaching the middle of the crown is 5 and 2 (as against 3 or 4 and 2 or 3), and the number of short ridges is 1 and 1 (as against 1, 2 or 3, and 2).

The crowns of the teeth of *Iguanodon* show a wide range of variation (Owen 1855, 1861*a*, 1874; Galton and Jensen 1975, 1979*a*) but appear to differ in a few respects from those of *Camptosaurus*. In *Iguanodon* teeth only one side of the crown is enamelled (Owen 1854), it is more elaborately sculptured, and the free edge of the small, plate-like marginal denticles are minutely mammillated (Hulke 1880), whereas in OUM J.3303 and *Camptosaurus* the margin is even. The teeth of *I. hoggii* Owen (1874) from the upper part of the Lulworth Beds (Lower Cretaceous, Berriasian; Dodson *et al.* 1964; Hallam 1975) of Dorset are the most similar, but in this species the dentary tooth crowns are proportionally more elongate and there are two very prominent vertical ridges at one-third and two-thirds crown width, rather than one that is about in the centre (pl. 52, figs. 7–9). The maxillary teeth of the iguanodontid *Priodontognathus phillipsi* (Seeley 1875*a*; CUM B.53408; see Lydekker 1893, pl. 11, fig. 3; may be from Upper Jurassic of Yorkshire) are very different from those of *Camptosaurus*: in medial view the crown is subtriangular with only a hint of a central vertical thickening, the marginal denticles are proportionately large and the cingulum consists of two crescentic flanges with small denticles along the lower edge. In *Tenontosaurus* the dentary teeth have the prominent keel that is completely lacking on the maxillary teeth, whereas in *Dryosaurus* the prominent keel is equally well developed on both sets of teeth (Janensch 1955; YPM 1876).

Stapes. The proximal 4·5 mm of the left stapes is preserved in the ventral part of the large foramen between the prootic and the opisthotic (text-fig. 1Y).

The preserved part is boot shaped and the expanded footplate has a maximum diameter of 4·0 mm and the minimum diameter of the broken end of the shaft is 1·5 mm. Originally the stapes was probably a slender rod connecting the fenestra ovalis to the tympanum, which was supported by the paroccipital process and the quadrate as described for the hadrosaur *Corythosaurus* (Colbert and Ostrom 1958; Ostrom 1961). The stapes is also preserved in the hadrosaur *Anatosaurus* (Colbert and Ostrom 1958), the hypsilophodontid *Dryosaurus* (HMN dy B), the theropod *Dromaeosaurus* (Colbert and Ostrom 1958), the prosauropods *Anchisaurus* (Galton 1976*a*) and *Plateosaurus* (Colbert and Ostrom 1958), and the discovery of a stapes in a skull of the sauropod *Camarasaurus* is reported by King (1978). Its absence from most dinosaur skulls is presumably a function of its fragility, because the more robust ceratobranchials are also rarely preserved.

Vertebral column

No information is available concerning the original order of the vertebrae, all of which are crushed or broken to a varying degree (text-figs. 4–7). Many of the vertebrae are preserved only as centra, the measurements of which are given in Table 1. The vertebral count is estimated as 9 cervicals, 16 dorsals, 6 sacrals, and about 45 caudals (text-fig. 3).

Cervical vertebrae (text-fig. 4A–J). There are 7 cervicals in addition to the missing atlas and third cervical, so that the total count was probably 9 as in *Camptosaurus*, *Dryosaurus*, and *Hypsilophodon* rather than 10 or 11 as in *Iguanodon* (Dollo 1883*b*, 1884; Hooley 1925), 11 as in *Ouranosaurus*, and 12 as in *Tenontosaurus*. All the cervical centra show some degree of crushing and are opisthocoelous with a convex anterior surface and a concave posterior surface. A strong ventral keel that widens slightly anteriorly and more markedly posteriorly is present on cervicals four to nine. The parapophysis is very low on the axis, lies just below the neurocentral suture on the fourth and fifth cervicals, and is bisected by it on the remaining cervicals. The corresponding cervicals of *Camptosaurus* are opisthocoelous with the concavity either more strongly (USNM 5473) or more weakly developed (USNM 5474) and the centra are less angular in anterior view (Gilmore 1909).

EXPLANATION OF PLATE 52

Teeth and cranial bones of *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 (1–4, 7–9, 14–16) and teeth of *C. dispar* (Marsh), holotype YPM 1877 (11) plus referred specimens YPM 7416 (5, 7, 12) and USNM 4281 (10). Maxillary teeth illuminated from below to show ornamentation more clearly.

Figs. 1–4, teeth of middle of right maxilla, × 2; 1, medial view of erupting crown; 2, lateral view of 1, 3, lateral view of fully erupted crown; 4, anterior view of 3.

Figs. 5, 6, teeth of right maxilla, × 2; 5, medial view; 6, lateral view.

Fig. 7, teeth on posterior part of right dentary in medial view, × 2; these teeth were the basis of the reconstruction by Hulke (1880, pl. 18, fig. 8).

Fig. 8, second tooth from posterior end of left dentary in medial view, × 2 (tooth a in Fig. 17).

Fig. 9, tenth tooth from posterior end of left dentary in medial view, × 2 (tooth b in Fig. 17).

Fig. 10, teeth on posterior part of right dentary in medial view, × 2.

Fig. 11, middle dentary tooth in medial view, × 1·5.

Fig. 12, tooth on right maxilla in medial view, × 2.

Fig. 13, stereophotographs of right maxilla in dorsal view (cf. text-fig. 1M), × 0·5.

Fig. 14, left maxilla in dorsal view (cf. text-fig. 1L), × 0·5.

Fig. 15, left jugal in medial view (cf. text-fig. 1G), × 0·5.

Fig. 16, right premaxilla in medial view (cf. text-fig. 1B), × 0·5.

Fig. 17, posterior part of left dentary in medial view, × 0·5. For teeth a and b see Figs. 8 and 9.

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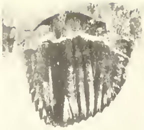
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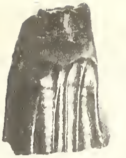
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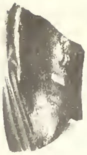
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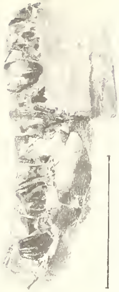
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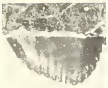
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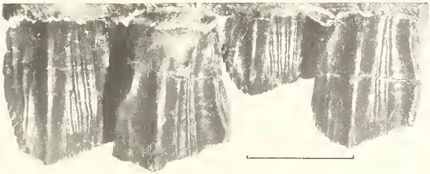
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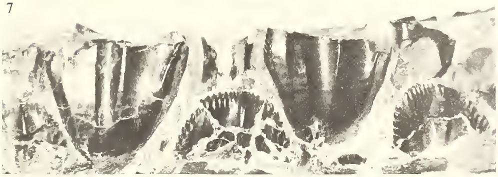
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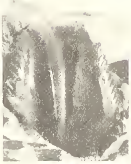
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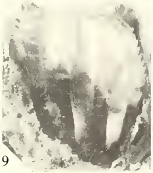
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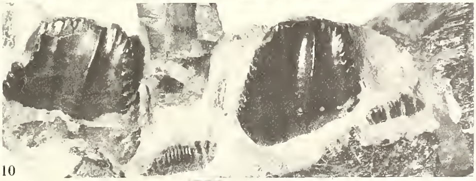
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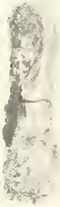
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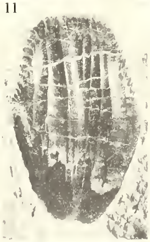
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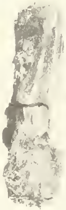
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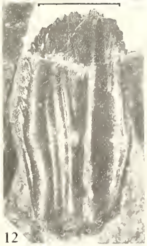
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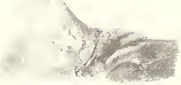
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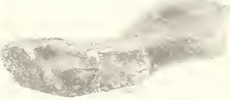
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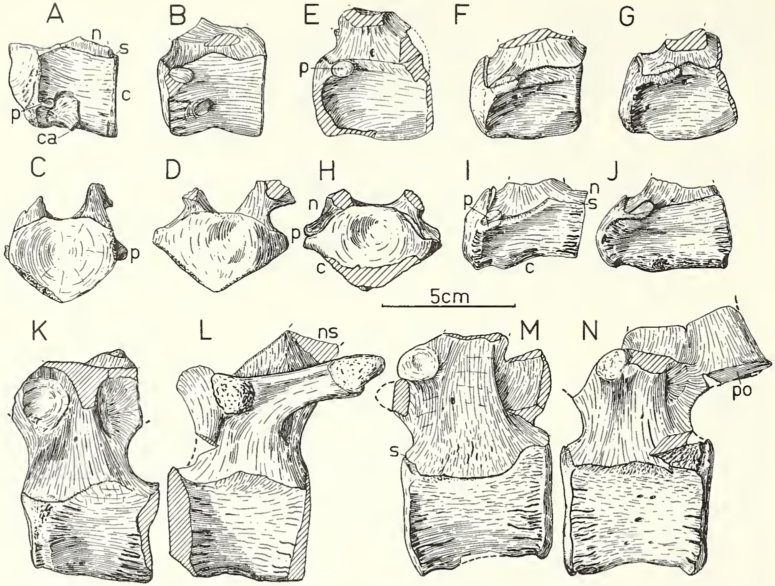
GALTON and POWELL, dinosaur *Camptosaurus*

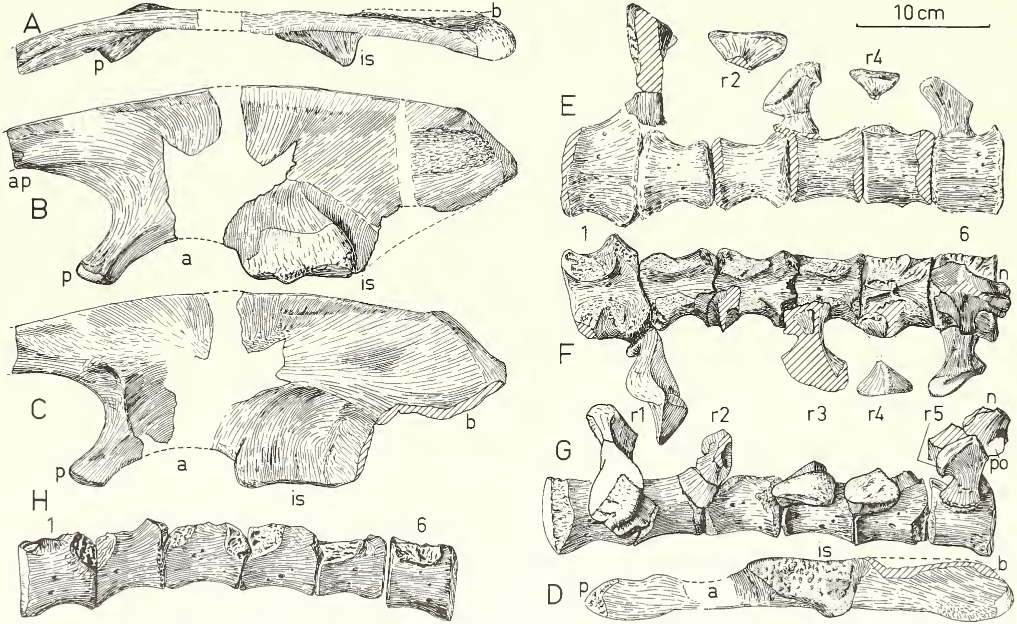


TEXT-FIG. 4. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–J, cervical vertebrae: A, second (axis) with proximal end of left rib (displaced and with medial surface exposed); B, C, fourth; D, E, fifth (see also Hulke 1880, pl. 19, figs. 1–4); F, sixth; G, H, seventh; I, eighth; J, ninth; K–N, dorsal vertebrae: K, fifth; L, seventh; M, ninth; N, twelfth. Views—left lateral (A, B, E–G, I–N), anterior (D, H), and posterior (C). Abbreviations: c, centrum; ca, capitulum; ch, facet for centrum; d, diapophysis; n, neural arch; ns, neural spine; p, parapophysis; po, postzygapophysis; pr, prezygapophysis; s, suture.

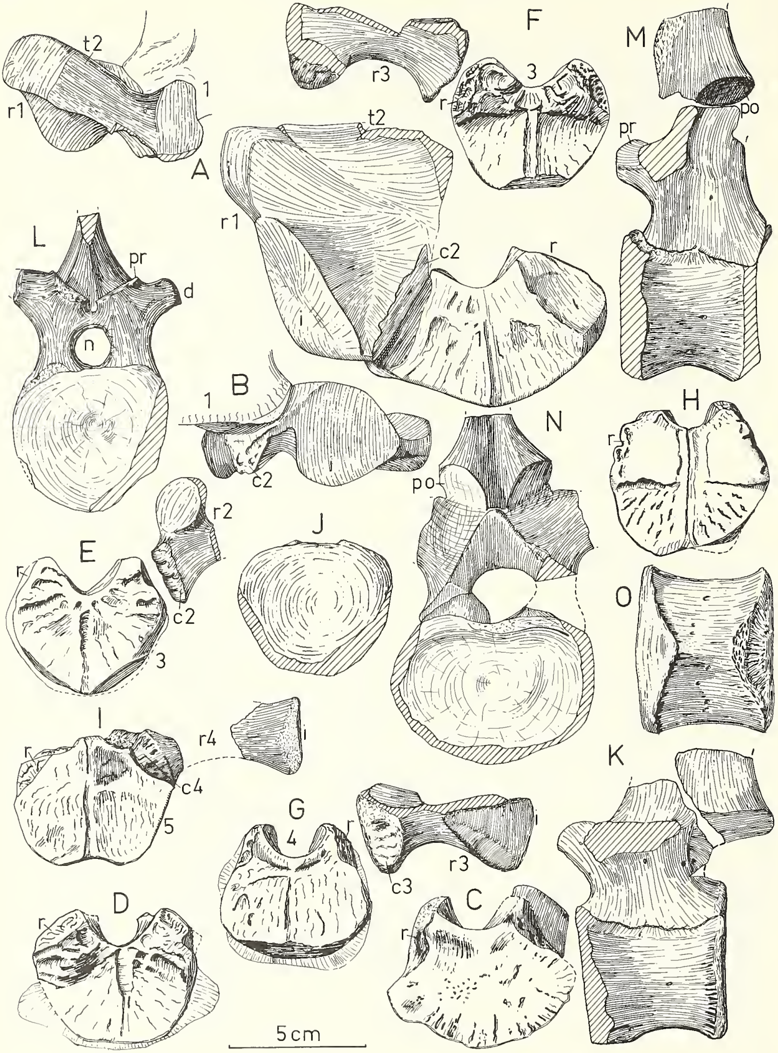
Dorsal vertebrae (text-figs. 4K–N, 6K–N). If the sacro-dorsal vertebra supporting the anterior surface of the first sacral rib is included as a functional part of the sacrum, then there are 16 dorsal vertebrae as in *Camptosaurus* (Gilmore 1925) whereas there are 14 or 15 in *Hypsilophodon*, 15 in *Dryosaurus*, *Tenontosaurus*, and *Thescelosaurus*, 16 or 17 in *Iguanodon* (Dollo 1883*b*, 1884; Hooley 1925), and 17 in *Ouranosaurus*.

The degree of convex curvature of the anterior surface of the centrum decreases in the first two vertebrae and increases in the next two, whereas the posterior surface becomes progressively less concave. The ventral keel becomes progressively less concave. On the fourth dorsal centrum and on the succeeding centra the concavity of the posterior surface is slightly greater than that of the anterior surface. The ventral keel becomes progressively less pronounced on the first five centra posterior to this, the ventral surface is rounded and the centra becomes progressively more massive. The first four dorsals are represented only by centra, but the fifth is more complete and is similar to the third dorsal of *Camptosaurus* (Gilmore 1909, fig. 15). On the seventh dorsal (text-fig. 4L) the parapophysis is at the base of the transverse process, whereas on the ninth, twelfth, and thirteenth dorsal vertebrae it is completely on the transverse process. The fourteenth dorsal is similar to the thirteenth of *Camptosaurus* (Gilmore 1909, fig. 16). In dorsal vertebra fifteen and sixteen the base of the transverse process is higher on the neural arch.

Sacrum (text-figs. 5E–H, 6A–J, 7A–E). The sacrum as a functional unit has six vertebrae with a massive sacro-dorsal anteriorly and a sacro-caudal posteriorly. The rib of the sacro-caudal contacted the ilium but the adjacent



TEXT-FIG. 5. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. A, B, left ilium; C, D, right ilium; E–G, sacral vertebrae and ribs; H, restoration of sacral centra. Views—left lateral (B, G, H), medial (C), dorsal (A, F), and ventral (D, E). For dorsal and ventral views of sacral centra 1 to 5 see also Hulke (1880, pl. 36, figs. 1, 2). Abbreviations: a, acetabulum; ap, anterior process; b, brevis shelf; c, surface for centrum; ch, facet for chevron; d, diapophysis; i, surface for ilium; is, surface for ischium; n, neural arch; p, public peduncle; po, postzygapophysis; pr, prezygapophysis; r, surface for sacral rib; r1–5, sacral ribs 1 to 5; s, suture; t, transverse process; t2, transverse process of second sacral vertebra; 1–6, centra of sacral vertebrae 1 to 6.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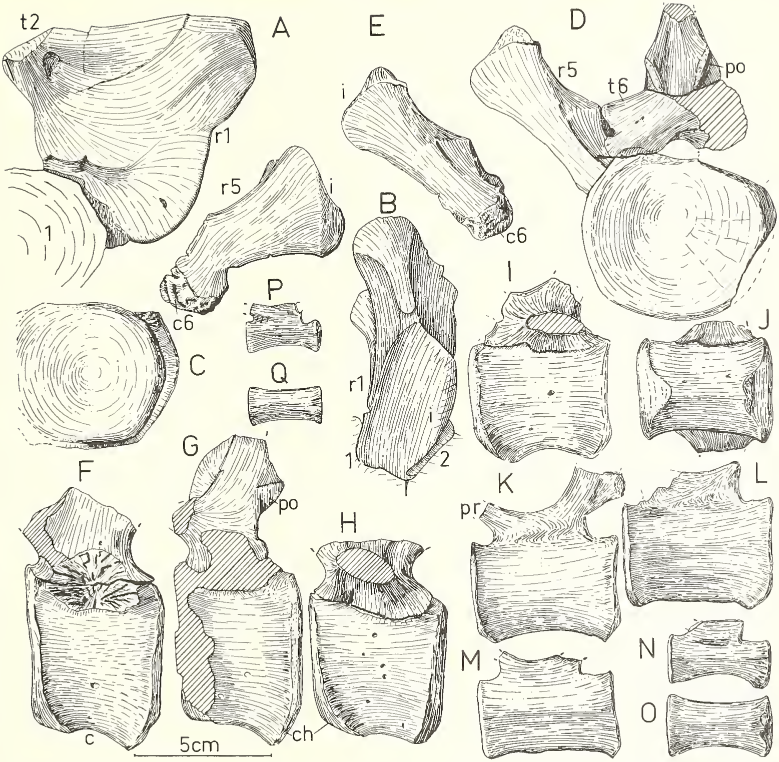


TEXT-FIG. 7. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–E, sacral vertebrae and ribs; A, B, left sacral rib; C, D, sixth sacral vertebra and left fifth sacral rib; E, left fifth sacral rib; F–Q, caudal vertebrae: F, second; G, third; H, fourth; I, J, ninth; K, fourteenth; L, seventeenth; M, twentieth; N, O, thirtieth; P, Q, thirty-fourth. Views—anterior (A, C), posterior (D, E), left lateral (F–I, K–N, D) and ventral (O, Q). For G see also Hulke (1880, pl. 19, fig. 9), for abbreviations see text-fig. 4. For caudals 18, 30, and 35 see also Hulke (1880, pl. 19, figs. 11–13).

TEXT-FIG. 6. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5. A–J, centra and ribs of sacral vertebrae; A, dorsal view of left first sacral rib and posterior view of same rib and centrum of first sacral vertebra; B, ventral view of left first sacral rib; C, D, second sacral centrum; E, third sacral centrum and base of second left sacral rib; F, third sacral centrum and third left sacral rib; G, fourth sacral centrum and third left sacral rib; H, fourth sacral centrum; I, fifth sacral centrum and fourth sacral rib; J, fifth sacral centrum; K–N, dorsal vertebrae; K, fifth; L, fourteenth; M–N, sixteenth; O, centrum of third caudal vertebrae. Views for C–O: anterior (C, E, G, I, L), posterior (D, F, N, H), left lateral (K, M) and ventral (O). For abbreviations see text-fig. 5.

surfaces of the last two sacral centra are gently concave and were not co-ossified. The sacral count varies in several genera of ornithopods, being either six of seven in *Camptosaurus* (USNM 2210; YPM 1877a; USNM 4282), *Hypsilophodon*, *Iguanodon*, and *Tenontosaurus*. Ostrom (1970) notes that the degree of fusion of the sacral vertebrae varies in different specimens of *Tenontosaurus*.

The form of the sacral centra resemble those of *Camptosaurus* (USNM 2210; YPM 1877a; Gilmore 1909) in most respects. The first centrum has a median ventral keel, which is more strongly developed anteriorly, the second has a much weaker median keel, the third to fifth have a median longitudinal groove, and the sixth is gently convex with a ventrally protruding rim. The facets for the first four sacral ribs are intervertebral, with the fifth borne completely on the last sacral vertebra. The neural canal of the first four centra is transversely wide, with that of the last two constricted (text-fig. 5F) as in *Camptosaurus* (YPM 1877a). The sacral centra do not show the well-defined peg-and-notch articulation of some of the specimens of *Camptosaurus*, but the slight development of such an articulation between sacrals two and three and three and four approaches the condition in USNM 2210 (Gilmore 1909). The form of the ribs and their interrelations to the centra and the ilium is shown, but unfortunately little information is available concerning these ribs in *Camptosaurus*. Part of the transverse process of the second sacral vertebra is attached to the large first sacral rib which, judging from the figures in Gilmore (1909, figs. 17, 39), is similar to that of *Camptosaurus*.

TABLE 1. *Camptosaurus prestwichii*, OUM J.3303, measurements of vertebral centra in mm. C, caudal vertebra; CE, cervical vertebra; D, dorsal vertebra; HA, maximum height at anterior end; HP, maximum height at posterior end; L, maximum length; S, sacral vertebra; WA, maximum width at anterior end; WP, maximum width at posterior end; ( ), measurement approximate; +, measurement a minimum value as eroded; a, measured from floor of neural canal to ventral edge; b, includes chevron facet.

	L	HA	WA	HP	WP
CE2	42	(31)	(32)	(30)	(28)
CE4	42	28	44	31	40
CE5	45	28	50	33	41
CE6	44	31·5	51	32	46
CE7	45	31	53	33	(43)
CE8	46	35	54	(32)	(50)
CE9	50	(27)	(58)	(32)	(51)
D1	53	(33)	(55)	(30)	(51)
D2	(51)	(30)	44	—	(44)
D3	50	35	40	—	39
D4	—	—	—	—	45
D5	51·5	36	34	38	+38
D6	55	40	(32)	—	(35)
D7	54	42	+38	(40)	+38
D8	58	42	40	(44)	(37)
D9	57	46	(36)	46	(45)
D10	58	46	44	49	47
D11	55	50	44	(52)	48
D12	55	50	52	51	57·5
D13	59	52	(53)	(53)	61
D14	55	54	58	55	70
D15	54	56	68	56	(65)
D16	55	55	64	52	74
S1	55	53[a]	(66)	46	71
S2	54	43[a]	67	37[a]	(62)
S3	(55)	37[a]	57	39[a]	58
S4	52	38[a]	54	47[a]	58
S5	51	46[a]	57	50[a]	58
S6	48	53	59	59	70
C1	45	—	—	—	—
C2	51	(60)	60	65	59
C3	46	55	54	62[b]	51

	L	HA	WA	HP	WP
C4	51	55[b]	50	55[b]	46
C5	51	52[b]	46	51[b]	46
C6	46	48[b]	45	48[b]	42
C7	52	48[b]	44	—	41
C8	55	49[b]	43	49[b]	38
C9	53	45[b]	(38)	45[b]	41
C10	53	45	40	45	40
C11	51	43	42	43	42
C12	50	41	43	40	(43)
C13	53	40	43	41	41
C14	53	37	39	39	41
C15	53	36	40	39	39
C16	53	36	36	39	—
C17	54	37	36	38	(36)
C18	54	34	38	36	(34)
C19	53	32	37	34	33
C20	50	29	32	31	31
C21	49	28	30	30	27
C22	50	29	(29)	30	28
C23	48	27·5	30	—	(28)
C24	47	25	29	28	26
C25	46	25	27	25	25
C26	44	23	27	—	—
C27	43	(22)	(27)	(20)	24
C28	40	18	23	19	23
C29	41	20	(21)	19·5	22
C30	38	18	23	18	22
C31	37	16·5	(22)	(16)	(19)
C32	33	14	18	13	17
C33	30·5	13	17	12	15
C34	27	12	15	11	13
C35	25	11	13	10	12
C36	—	10	11·5	—	—

Caudal vertebra (text-figs. 6o, 7f–q). Remains of thirty-six caudals are preserved (text-fig. 3) and the original count was probably at least forty-five, as Gilmore (1909) estimated for *Camptosaurus*. Several progressive changes are observable in the series. The centra become progressively lower but, allowing for distortion from crushing and breaks, the length remains approximately the same until about caudal twenty-two and then decreases (Table 1). The second caudal shows a sutural area on the neural arch and centrum for the transverse process; on the third caudal this is just on the neural arch, and on the fourth caudal it is further on the arch. As in *Camptosaurus*, the transverse processes become progressively smaller, being vestigial on the twelfth and absent on the thirteenth caudal. The anterior and posterior surface of the anterior centra are equally concave but, posterior to the fifteenth, the posterior surface is more concave. On the first twelve centra the anterior chevron facet is slightly larger than the posterior one but, posterior to this, the reverse is the case; posterior to caudal twenty, only the posterior remains. The antero-ventral end of the posterior chevron facet is single anterior to caudal eight and double from there on posteriorly. Posterior to caudal fifteen, there is a lateral longitudinal ridge along the middle of the centra, the ends of which change from circular to approximately hexagonal in outline.

TABLE 2. *Camptosaurus prestwichii*, OUM J.3303, measurements of appendicular skeleton in mm.

	L	WP	WD
Humerus	297	83	64
Radius	—	46	36
Ulna	—	58	41
Femur	—	124	122
Tibia	—	161	143
Fibula	—	82	44

	WP	PA	PT	WD	DA	DT
MT I (left)	23	45	23	—	—	—
MT I (right)	21	40	21	—	—	—
MT II	—	81	31	—	53	44
MT III	—	68	48	—	47	58
MT IV	57	49	47	59	52	47

DA, antero-posterior diameter of distal end; DT, transverse diameter of distal end; L, maximum length; MT, metatarsal; PA, antero-posterior diameter of proximal end; PT, transverse diameter of proximal end; WD, maximum width of distal end; WP, maximum width of proximal end.

Appendicular skeleton

Pectoral girdle and fore-limb (text-fig. 8). The scapula is longer than the humerus as in *Camptosaurus*, *Dryosaurus altus* (Shepherd *et al.* 1977), *Ouranosaurus*, *Tenontosaurus*, and *Iguanodon* rather than being subequal as in *Othnielia*, *Hypsilophodon*, and *Dryosaurus lettowvorbecki*, or shorter as in *Thescelosaurus* (Galton 1974*b*). The incomplete dorsal end may have been posteriorly expanded as in *Camptosaurus*. Medially there is a foraminal groove which, according to Gilmore (1909), is only present in *Camptosaurus* and *Laosaurus* but which is also present in *Hypsilophodon*, *Ouranosaurus*, and *Iguanodon*. The coracoid has a foraminal notch as in *Camptosaurus* (Gilmore 1909; USNM 4282), rather than a complete foramen as in most other ornithopods. However, this is a variable feature in *Camptosaurus*, because in YPM 1877 the foramen is complete. A notch is present in some specimens of *Iguanodon* (Dollo 1882*a*; Hooley 1925).

A pair of incomplete bones may be part of either the pectoral girdle or the sternum. Each bone (text-fig. 8e–h) is triangular in section with a rounded end which, judging from its texture, was originally covered with cartilage. The thick edge is moderately flat with diagonally inclined striations. The paired sternal bones are known in only a few ornithopods, and there are two distinct patterns: either two thin crescentic plates together forming a shield-like structure, or two long, rod-like bones set at right angles to each other with contact between the median part of the thinner, transversely expanded, anterior end. The first pattern occurs in *Dryosaurus* (Gilmore 1925 as *Laosaurus*; Janensch 1955), *Othnielia*, *Hypsilophodon*, *Parksosaurus*, and *Tenontosaurus*. The second pattern occurs in *Camptosaurus* (YPM 1877), *Ouranosaurus*, *Iguanodon* (Dollo 1882*b*), and the hadrosaurs (Lull and Wright 1942). However, the paired bones described here are probably not sternal bones because they are proportionally too small and do not resemble any part of the sternal bones of either pattern. Sternal ribs are known for very few ornithopods. These are formed from ossified cartilage in *Othnielia*, *Hypsilophodon*, and *Thescelosaurus*, but in *Parksosaurus* the third and fourth sternal ribs are large pieces of bone. A third possibility to be considered is that these bones are clavicles, for which there is a distinct facet on the antero-ventral part of the scapula in most ornithischians. However, this is considered unlikely because in *Leptoceratops*, the only ornithischian for which a clavicle has been described (Brown and Schlaikjer 1940), it is rod-like and pointed at both ends. The paired bones are not sacral ribs, because these are all acounted for (text-fig. 5e–g) and they do not correspond to any cranial element. Although the form is not the same as those of *Parksosaurus*, the paired bones are tentatively identified as the anterior end of a left and right sternal rib.

The humerus (text-fig. 8L–O) is a little crushed and it has a low deltopectoral crest as in *Camptosaurus* (text-fig. 2K, L), *Dryosaurus* (Janensch 1955; Shepherd *et al.* 1977), and *Othnielia* but, because of its slenderness, it looks more like that of the hypsilophodontids *Dryosaurus* and *Othneilia*. The humerus is more slender than those of *Ouranosaurus*, *Iguanodon*, *Tenontosaurus*, and *Thescelosaurus*. The incompletely preserved radius and ulna (text-fig. 8P–Z) are also slender. The only identifiable element from the manus is a small piece (text-fig. 8I–K) that is tentatively identified as the ventro-lateral corner of the proximal end of metacarpal II. Hulke (1880) considered that the metacarpals were slender, a feature Gilmore (1909) noted was more suggestive of *Iguanodon* than of *Camptosaurus*, but this was based on pieces now identified as the radius. The measurements of the bones of the pectoral girdle and limbs are given in Table 2.

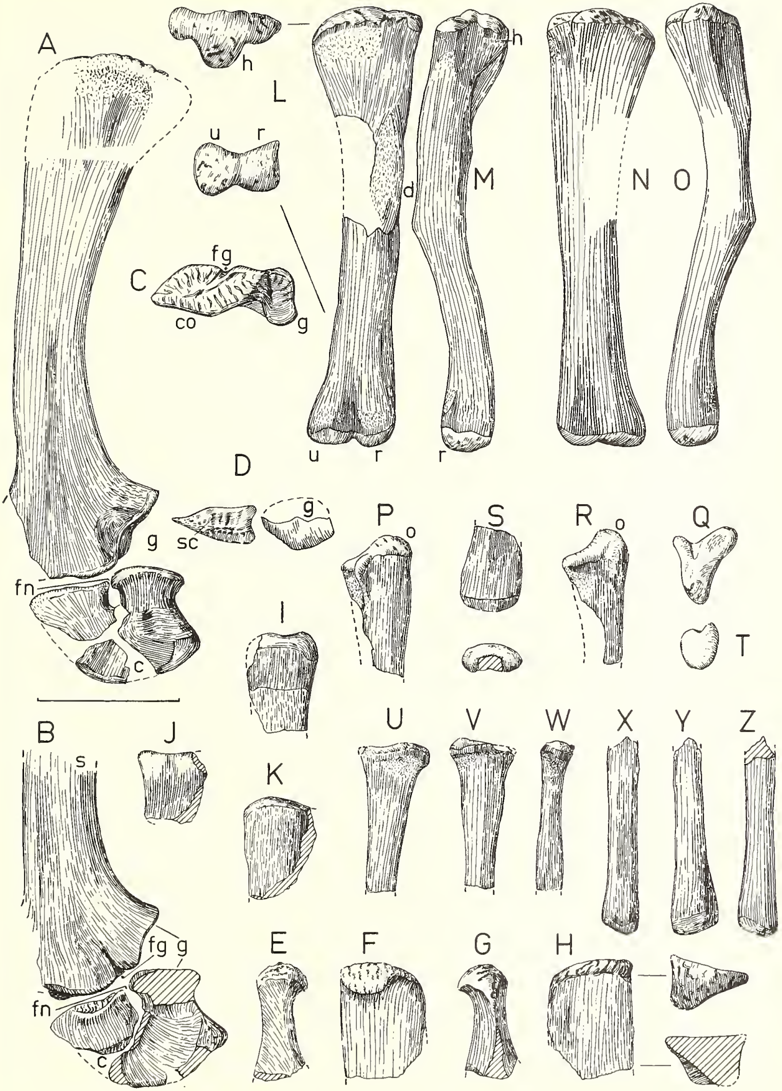
Pelvic girdle and hind-limb. The incomplete pelvic girdle resembles that of *Camptosaurus* (text-fig. 2C–E). The ilium (text-fig. 5A–D) has a deep blade, a massive ischiadic head, and a narrow brevis shelf. The pubis (text-fig. 9A–H) has a deep blade-like anterior process, and probably a long subacetabular part. Because of the expanded form of the distal end, which has a flat medial surface, the post-pubic rods were probably long with united distal ends. The ischium (text-fig. 9I–O) has a proximally placed obturator process. The flat medial surfaces of the bar-shaped distal ends were united to each other. The massiveness of the distal end of the ischium is intermediate between those of YPM 1888a (text-fig. 2C) and AMNH 6120 (Gilmore 1909, pl. 19).

The pelvic girdle of *Dryosaurus* (Galton 1977*a*, *b*) is similar to that of the Cumnor ornithopod, but the posterior part of the ilium is low, the brevis shelf is wide, and the anterior process of the pubis is more rod-like. In *Othnielia*, *Hypsilophodon*, and *Thescelosaurus* (Galton 1974*b*) the anterior process is even more rod-like and the distal part of the ischium is dorso-ventrally flattened and laterally expanded. In *Tenontosaurus* the dorsal margin of the ilium shows a distinct step, so the posterior part of the blade is deep, and the distal part of the ischium is more blade-like. In *Ouranosaurus* the pubis is proportionally much longer and the ilium smaller. In *Iguanodon* the ilium is similar in some specimens (Lydekker 1890*b*) and the anterior process of the pubis is comparably expanded (Dollo 1882*a*) or extremely large (Dollo 1882*a*; Hooley 1925). In *Iguanodon* (Dollo 1882*a*), *Ouranosaurus*, and *Tenontosaurus* the post-pubic rod is much shorter than the ischium.

Most of the bones of the hind-limb are represented (text-figs. 10–13), but only the ends of the long bones and of the metatarsals are preserved. The femur (text-fig. 10A–F) has a well-developed distal anterior intercondylar groove as in *Camptosaurus* (text-fig. 2F, H). This groove is deeper than it is in most femora of *Dryosaurus* (for range of variation see Galton 1977*a*, *b*). In *Othnielia* and *Hypsilophodon* there is no such groove, in '*Camptosaurus*' *leedsi* it is small (text-fig. 2G), in *Thescelosaurus* it is broad but shallow, and in *Ouranosaurus* and *Iguanodon* (Owen 1855; Galton and Jensen 1979*a*) it is very deep with the edges overhanging the groove. The massive femur of *Cryptodraco* Lydekker, 1889 (type species *Cryptosaurus eumerus* Seeley, 1875*b*; CUM J.46882) from the Oxfordian (Upper Jurassic) of Great Grandsen, seven miles east of St. Ives, Huntingdonshire, has a greater trochanter that is only half the antero-posterior width of the head, and distally the anterior intercondylar groove is shallow. The ends of the fibula and tibia (text-figs. 10G–L, 11A, J–L) are of the standard ornithopod pattern. The proximal end tapers more, so the tibia was probably more slender than that of *Camptosaurus*.

The astragalus and calcaneum (text-fig. 11A–I) are of the standard ornithopod pattern (cf. Galton 1974*a*). The pronounced depression on the anterior surface of the ascending process is also present on the astragali of *Camptosaurus* (YPM 1877) and *Dryosaurus* (YPM 1884). A large, cushion-shaped bone (text-fig. 13A–D) is similar to the large distal tarsal (fused II and III) of *Camptosaurus* (YPM 1877) and *Dryosaurus* (YPM 1884).

TEXT-FIG. 8. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·5 (E–K) and × 0·25. A–D, scapula and coracoid A, left in lateral view; B, right in medial view; C, sutural surface of right scapula; D, sutural surfaces of right coracoid; E–H, proximal end of a left sternal rib in E, medial view; F, ventral view; G, lateral view; H, dorsal view with anterior end and posterior cross section; I, K, proximal end of ?second metacarpal in I, ?dorsal view; J, proximal end and K, ?medial view; L–O, left humerus in L, anterior view with proximal and distal ends; M, lateral view; N, posterior view; O, medial view; P–S, left ulna, P, proximal end in lateral view; Q, proximal end; R, as P in dorsal view; S, distal end in lateral view with distal view; T–Z, left radius, T–W proximal end in, T, proximal; U, medial; V, lateral and W, posterior (or ventral) views; X–Z, distal end in X, anterior (dorsal), Y, lateral and Z, posterior (ventral) views. Abbreviations: c, coracoid; co, surface for coracoid; d, deltopectoral crest; fg, foraminal groove; fn, foraminal notch; g, glenoid cavity; h, head; o, olecranon process; r, radial condyle; s, scapula; sc, surface for scapula; u, ulnar condyle. Scale line represents 5 cm (E–K) or 10 cm.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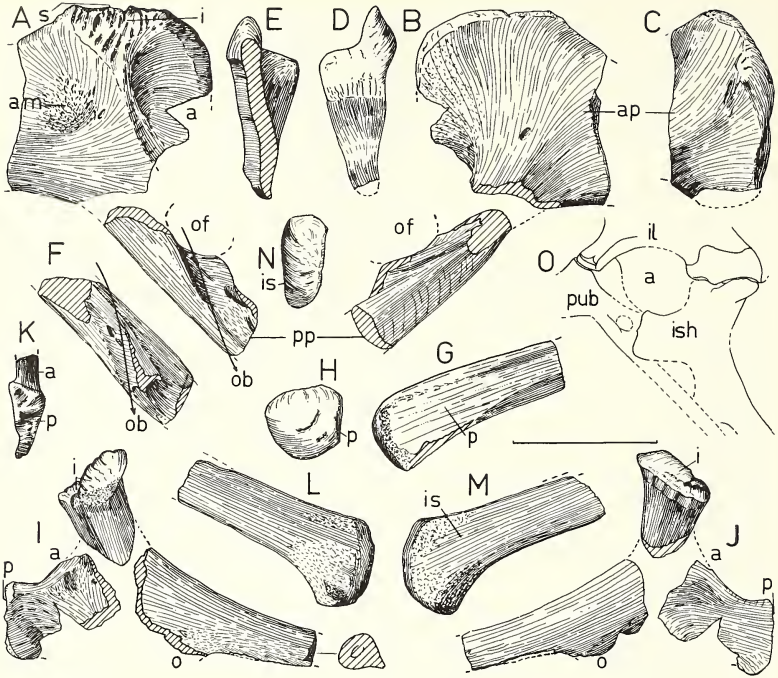


TEXT-FIG. 9. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. A–H, pubis × 0·5, A, acetabular part of left pubis in lateral view; B, as A in medial view; C, proximal end of right anterior pubis (prepubic process) in lateral view; D, as C, proximal end; E, reverse of D to show cross-section; F, dorsal view of anterior part of posterior pubis (postpubic rod); G, distal end of posterior process in medial view; H, distal end of posterior process; I–N, left ischium × 0·25, I, proximal end in lateral view; J, as I in medial view; K, proximal view of surface for pubis; L, distal end in lateral view; M, as L in medial view; N, distal end; O, reconstruction of acetabular region of pelvic girdle, compare with A, I and text-fig. 5B. Abbreviations: a, acetabulum; am, area of origin of M. ambiens (see Galton 1969); ap, anterior process; i, sutural surface for ilium; is, sutural surface for ischium; ish, ishium; o, obturator process; ob, route of obturator nerve and blood vessels; of, obturator foramen; p, sutural surface for pubis; pp, posterior process (postpubic rod) of pubis; s, sutural surface for first sacral rib. Scale line represents 5 cm (A–H) or 10 cm.

The pes is similar to that of *Camptosaurus* (text-figs. 2I, J, 11M, 12, 13). The proximal end of metatarsal I (text-figs. 12M, 13E) is proportionally more massive than it is in *Camptosaurus*, in which the complete bone is either short (text-fig. 2I) or long (Gilmore 1909, fig. 35). Metatarsals II and IV (text-fig. 13F–H, L) are very incomplete. Metatarsal III is reasonably complete (text-fig. 13I–K) and the ratio of the maximum antero-posterior width over the maximum length is between 0·4 (maximum value assuming no shaft lost) to 0.35 (more probable value) as against 0·39–0·46 for the more massive metatarsal III of *Camptosaurus* (USNM 4277; YPM 1877, 6801, 7355). This ratio is 0·15 in *Hypsilophodon*, 0·26 in *Dryosaurus* (YPM 1884), 0·27 in *Ouranosaurus*, and

0·34–0·51 in *Iguanodon* (Owen 1858; Dollo 1883*b*). The proximal end of metatarsal IV is less expanded transversely than is that of *Camptosaurus* (text-fig. 2I, J).

Most of the phalanges are represented and these are tentatively identified as shown (text-figs. 12, 13M–S). A small phalanx (text-fig. 12C–G) is similar to the first phalanx of digit I of *Camptosaurus* (text-fig. 2I, J) so this digit was reduced. In *Othnielia*, *Hypsilophodon*, *Tenontosaurus*, and *Thescelosaurus* this phalanx is longer than the first phalanx of digit II whereas in *Dryosaurus* (Galton 1977*a*, *b*; Shepherd *et al.* 1977), *Ouranosaurus* and *Iguanodon* (Dollo 1882*a*, 1883*b*) this digit is represented only by a vestigial metatarsal. The first phalanges of digits II and III are slightly more slender than are those of *Camptosaurus*. The width is greater than the length for the third and fourth phalanges of digit IV (text-fig. 12A, B, H–J) and this is also the case in *Camptosaurus* and *Iguanodon* (Dollo 1882*a*; Hooley 1925 in which phalanges 2 and 3 are incorrectly transposed). The reverse is true in *Othnielia*, *Dryosaurus* (Galton 1977*a*), *Hypsilophodon*, *Tenontosaurus*, and *Thescelosaurus*.

EUROPEAN SPECIES OF *CAMPTOSAURUS*

The four species of ornithopod dinosaurs from Europe that have been referred to the genus *Camptosaurus* Marsh (1885) are listed below and discussed in descending stratigraphical order.

Camptosaurus inkeyi Nopcsa (1900), Upper Cretaceous of Comitat Hunyad, Transylvania, Hungary; holotype, a dentary with part of angular.

C. valdensis Lydekker (1889), Lower Cretaceous (Wealden) of Isle of Wight, England; holotype, a left femur (BMNH R167); referred specimen, a dentary (BMNH R180).

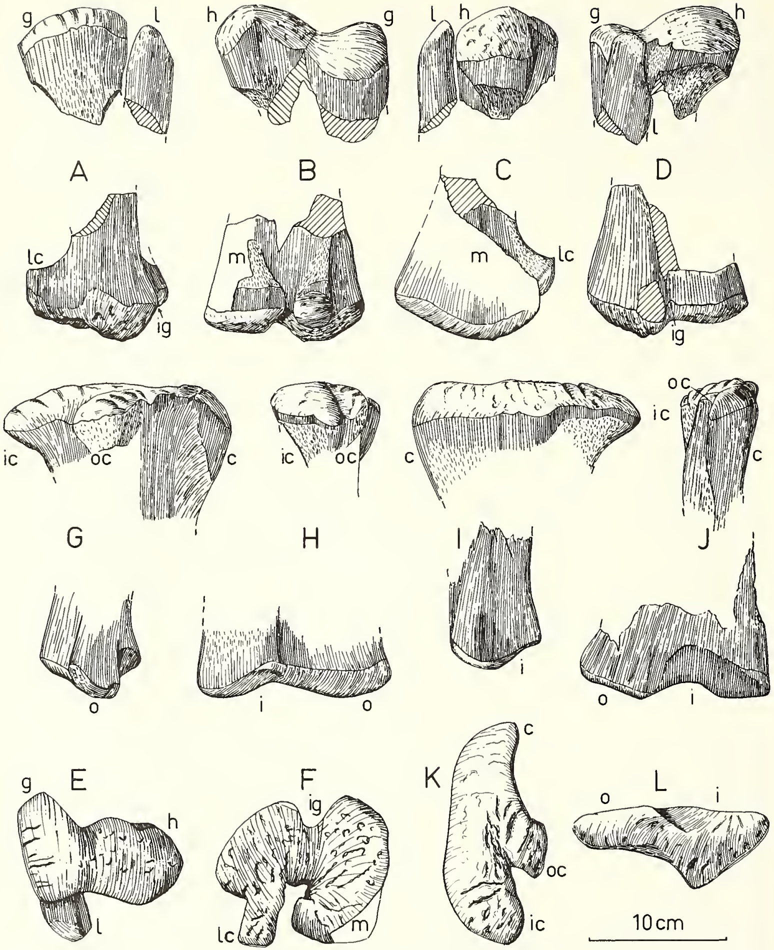
C. prestwichii Hulke (1880), Upper Jurassic (Lower Kimmeridgian) of Cumnor Hurst near Oxford, England; holotype, skeleton OUM J.3303 described above (text-figs. 1–13).

C. leedsi Lydekker (1889), Middle Jurassic (Upper Callovian) from near Peterborough, England; holotype, a left femur (BMNH R1993, text-fig. 2G).

1. *C. inkeyi* was described by Nopcsa (1900, p. 579) in a footnote. Gilmore (1909) listed the species as *C. ?inkeyi* but noted that the dentary as described was quite unlike those of the American species. However, a fuller description was promised, so he left the final disposition of this species to Nopcsa. The citation of *Camptosaurus* from the Upper Cretaceous of Europe by Steel (1969) and Charig (1973) is based on this specimen, which has never been figured and is probably lost. However, Nopcsa (1904) noted that the holotype of *C. inkeyi* is another specimen of *Rhabdodon* (= *Mochlodon*), the common iguanodontid from the Upper Cretaceous of Transylvania.

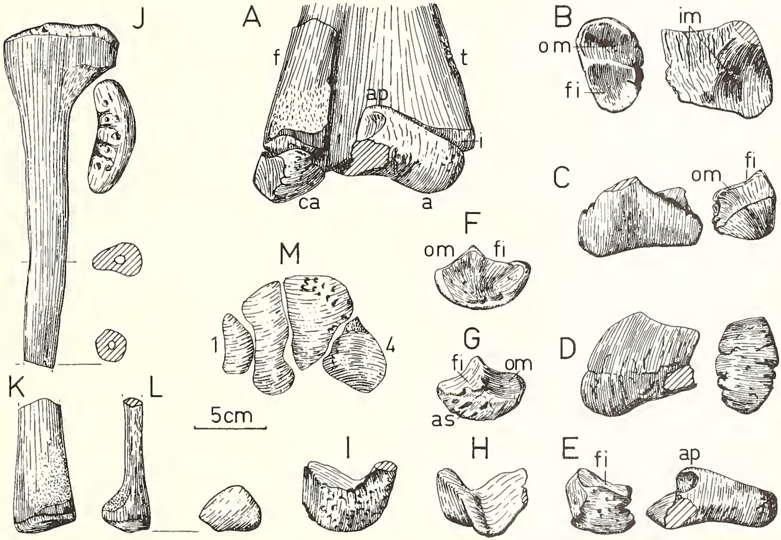
2. *C. valdensis* was described by Lydekker (1889), but the type femur was only recently figured by Galton (1974*a*) who concluded that it is from a large individual of *Hypsilophodon foxii*. Galton (1974*a*) followed Owen (1864) in regarding the mandibular ramus as that of a juvenile *Iguanodon*. However, this cannot be the case, because the posterior teeth are on the antero-medial edge of the coronoid process rather than medial to it as in *Iguanodon* (Galton 1976*b*). Galton (1976*b*) provisionally referred this dentary to the iguanodontid *Vectisaurus valdensis*, but now refers it to the hypsilophodontid *Valdosaurus* Galton (1977*a*, type species *Dryosaurus ?canaliculatus* Galton, 1975; an additional referred specimen is the *Dryosaurus*-like ilium (BMNH R2150) from the Wealden of Sussex that was figured by Lydekker (1888*a*) as *Hylaeosaurus*).

3. *C. prestwichii* (Hulke) is described above (text-figs. 1–13). The skeleton is the holotype of *I. prestwichii* Hulke (1880) but referral of this species to the genus *Iguanodon* is incorrect because it shows many differences from the other species of that genus. In *Iguanodon* (Dollo 1882*a*, *b*, 1883*a*, *b*, 1884; Owen 1855, 1858, 1861*a*, 1874; Hooley 1925; Casier 1960) the skull is tall and narrow, the supraoccipital is excluded from the margin of the foramen magnum, there are 21 to 23 tooth positions in each jaw (18 in a juvenile), the teeth are unenamelled on one side of the crown and the sculpturing on the other side is more complex, and the posterior teeth of the dentary are medial to the coronoid process rather than being on its anterior edge (see Galton 1976*b*). There are 10 or 11 cervicals and 17 or 16 dorsal vertebrae, the posterior process of the pubis is much shorter than the ischium, the anterior intercondylar groove at the distal end of the femur is tunnel-like with the sides overhanging it anteriorly, and metatarsal I is reduced to a splint with no phalanges (for contrasting situations in OUM J.3303 see p. 434).

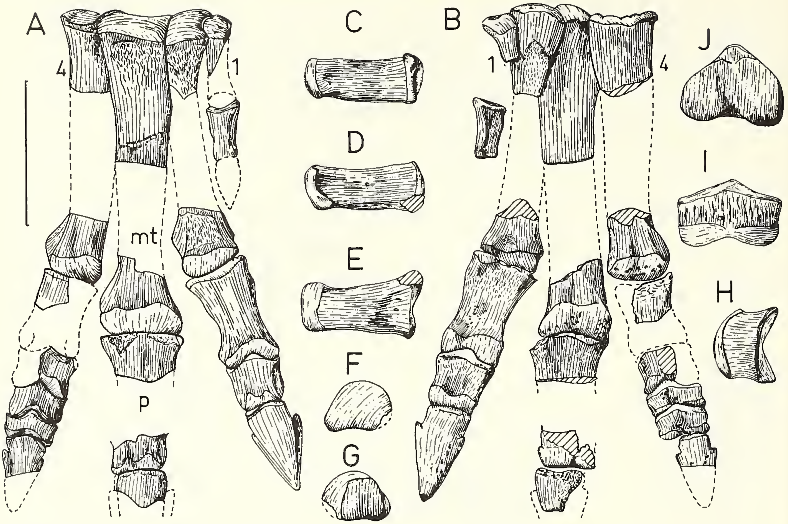


TEXT-FIG. 10. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. Right femur (A–F) and tibia (G–L) in lateral (A, G), posterior (B, H), medial (C, I), anterior (D, J), proximal (E, K), and distal views (F, L). For abbreviations see text-fig. 11.

The skeleton described as *I. prestwichii* by Hulke (1880) is readily distinguishable from the corresponding parts of the other ornithopod taxa described from the Upper Jurassic and the Lower Cretaceous of England. *Cryptosaurus eumerus* Seeley (1875*b*), the type species of the iguanodontid genus *Cryptodraco* Lydekker (1889), is based on a femur (CUM J.46882) from the Oxfordian (p. 428) that has a very narrow greater trochanter (half antero-posterior width of head) and distally the anterior intercondylar groove is broad and very shallow (cf. text-fig. 10E, F). The maxilla (CUM B53408) of *Priodontognathus phillipsii* (Seeley 1875*a*) may have come from the Upper Jurassic of Yorkshire and the teeth are very different from those of OUM J.3303 (see p. 420). Two ornithopods are described from the upper part of the Lulworth Beds of Dorset (= Middle Purbeck Beds, Lower Cretaceous, Berriasian, Dodson *et al.* 1964, Hallam 1975), *I. hoggii* Owen (1874) in which the dentary teeth have two prominent vertical ridges, and the fabrosaurid *Echinodon becklessii* Owen (1861*b*) in which the teeth lack secondary vertical ridges and are borne on a slender dentary and a maxilla with an almost flat lateral surface (Galton 1973*a*, 1978). *Hypsilophodon foxii* Huxley (1869) from the Wealden of the Isle of Wight differs from OUM J.3303 in the form of the skull, teeth, humerus, pelvic girdle, femur, and pes (see comparative section and Galton 1974*a*).



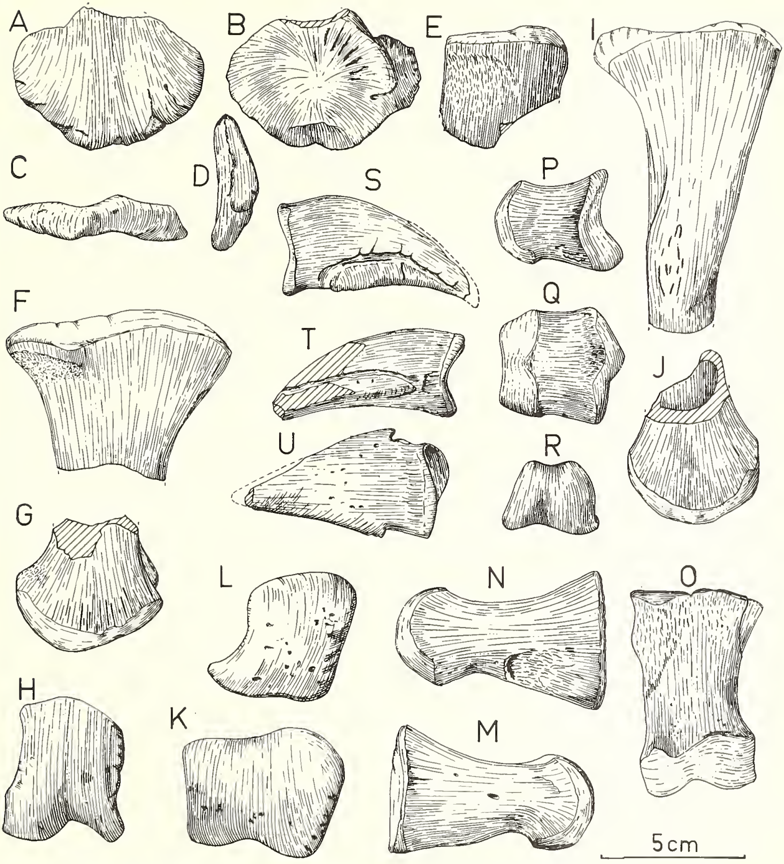
TEXT-FIG. 11. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303 × 0·25. Right hind-limb: A, distal end of tibia and fibula with proximal tarsals in anterior view; B–E, proximal tarsals in B, proximal; C, posterior; D, distal and E, anterior views; F, G, calcaneum and H, I, astragalus in lateral (F, H) and medial (G, I) views, J–L, fibula J, proximal part with end view and cross section; K, distal part in anterior view; L, as K in medial view with end view; M, proximal ends of metatarsus. For A, B, D, and F see also Hulke (1880, pl. 20, figs. 3–6). Abbreviations: a, astragalus; ap, ascending process; as, surface for astragalus; c, cnemial crest; ca, calcaneum; f, fibula; fi, surface for fibula; g, greater trochanter; h, head, i, inner malleolus; ic, inner condyle; ig, intercondylar groove; im, surface for inner malleolus; l, lesser trochanter; lc, lateral condyle; m, medial condyle; mt, metatarsal; o, outer malleolus; p, phalanx; t, tibia; 1–4, digits 1 to 4.



TEXT-FIG. 12. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. A, B, right pes (ends of metatarsals spaced a bit too far apart, see text-fig. 2); C–G, phalanx 1 of digit I in C, lateral; D, medial; E, ventral; F, distal and G, proximal views; H–J, phalanx 4 of digit IV in H, medial, I, ventral and J, distal views. For abbreviations see text-fig. 11. Scale line represents 10 cm (A, B ×0·25) or 5 cm (C–J ×0·5).

The skeleton OUM J.3303 is very similar to those of *Camptosaurus dispar* (see note p. 412) from the Upper Jurassic of North America, and the similarities are listed in the diagnosis of the genus *Camptosaurus* (p. 437). The skull is low and broad, the outlines of the bones are similar (text-fig. 2A, B) and the maxilla and dentary each bear about sixteen teeth, the form of which is very similar in both species (pl. 52, figs. 1–12). The vertebrae are similar with the same number in each region. The scapula is longer than the humerus, which has a low deltopectoral crest (text-fig. 2K–M). The ilium is deep with a narrow brevis shelf, the anterior process of the pubis is evenly expanded and blade-like, the post-pubic rod is long, and the distal part of the ischium is rod-shaped (text-fig. 2C, D). Distally the femur has a well-developed anterior intercondylar groove (text-fig. 2F, H). In the pes, the phalanges of digit I are reduced and the width of the third and fourth phalanges of digit IV is greater than the length (text-fig. 2I, J).

The differences between *Camptosaurus dispar* and *C. prestwichii* are listed (p. 438) and given below (Table 3). There are differences in the proportion of the skulls and of the individual bones (text-fig. 2A, B) but these are less than those shown within the genus *Iguanodon* (see Dollo 1883*b*, 1884; Casier 1960; Hooley 1925). The small size of the intramaxillary cavity of *C. prestwichii* is an important character, but the difference in the maxillary teeth is minor and could be an individual variation of the English specimen. The difference in the outline of the anterior end of the centra of cervical vertebrae four to nine is a valid difference. *C. prestwichii* is more gracile than the very massive *C. dispar* (text-fig. 3; figures of skeletons in Gilmore 1909, 1912) and this is reflected in the more slender form of the limb bones and in particular the humerus, tibia, and metatarsals (text-fig. 2I–M). Numerous species of



TEXT-FIG. 13. *Camptosaurus prestwichii* (Hulke), holotype OUM J.3303. Right pes × 0·5. A–D, medial distal tarsal in A, proximal; B, distal; C, posterior and D, medial views; E, proximal end of metatarsal I in medial view; F, proximal part of metatarsal II in medial view; G, distal part of metatarsal II in medial view; H, as G in distal view; I, proximal part of metatarsal III in medial view; J, distal part of metatarsal III in medial view; K, as J in distal view; L, distal end of metatarsal IV; M–O, phalanx 1 of digit II in M, lateral; N, medial and O, ventral views; P–R, phalanx 2 of digit II in P, medial; Q, ventral and R, distal views; S–U, ungual phalanx of digit II in S, lateral; T, medial and U, ventral views.

TABLE 3. Comparison of skeletal characters of *Camptosaurus dispar* and *C. prestwichii.*

Character	*C. dispar*	*C. prestwichii*
Intramaxillary cavity	Large	Small
Number of secondary ridges reaching middle of maxillary tooth crown anterior to prominent keel	3 or 4	5
Anterior end of cervical centra 4 to 9	Less angular, rounded ventrally	Subrhomboidal
Peg-in-notch articulation between sacral centra	Weakly to strongly developed	Weakly developed
Long bones	Robust	Slender
Anteroposterior expansion of proximal end of metatarsals I, II, and III	I reduced, II and III much expanded	I not reduced, II and III slightly expanded

Iguanodon have been described from the Lower Cretaceous of western Europe (see Steel 1969), but Ostrom (1970) concluded that there were only two or three morphological—if not valid taxonomic—entities, which include a smaller and slender *Iguanodon* (e.g. single *I. mantelli* skeleton in Brussels, see Dollo 1882*a*, 1884; Casier 1960; *I. atherfieldensis* Hooley, 1925) and a larger more robust *Iguanodon* (e.g. several skeletons of *I. bernissartensis*, see Dollo 1882*a*, 1883*a*; Casier 1960). These two osteological types of *Iguanodon*, regarded as male and female of the same species by Nopcsa (1929), show more differences in the form of the skull, girdles, and limbs than do skeletons of *C. prestwichii* and *C. dispar*. Given the range of variation within the ornithopod genus *Iguanodon*, we consider that the differences shown (Table 3) do not justify recognition of the genus *Cumnoria* Seeley (1888) for *I. prestwichii* Hulke (1880) which instead is referred to the genus *Camptosaurus* Marsh (1885) as *C. prestwichii* (Hulke).

A few other specimens described from the Upper Jurassic of Europe have been referred to *C.* (*Iguanodon*) *prestwichii*. Lydekker (1886) figured a tooth as *I. prestwichii* but this is incorrect, because the drawing is reproduced from Dollo (1885) in which it is labelled as an *Iguanodon* tooth from the Lower Cretaceous (*I. mantelli* from text). Sauvage (1888, pl 12, fig. 5; 1897–1898, p. 7, figs. 11, 12) illustrated a fragmentary tooth of *I. prestwichii* from the Upper Jurassic (Upper Portlandian) of Boulogne-sur-Mer, France. The sides of the crown diverge from the root, the prominent keel is in the centre and the root shows a resorption area on the ornamented side of the tooth. This is a dentary tooth and it may be from the left side. Four ridges reach the base of the crown on the ornamented side, so the ridges are more numerous and pronounced than on teeth of *C. prestwichii* (pl. 52, figs. 7–9). The unworn base of the other side of the crown has two centrally located vertical ridges that are close together and continue on to the adjacent part of the root. In *Camptosaurus*, ornamentation on this side of the tooth is restricted to a few short terminal ridges (pl. 52, figs. 1, 5). This tooth is identified as iguanodontid, generically and specifically indeterminate.

Sauvage (1888, 1897–1898) also referred five vertebrae from the Upper Jurassic of Boulogne-sur-Mer to *I. prestwichii*. A caudal vertebra (Sauvage 1897–1898, pl. 7, figs. 7–12) was classified by Nopcsa (1928) as that of a theropod dinosaur and is the holotype of the coelurid taxon *Caudocoelus sauvagei* von Huene (1932). Four sacral vertebrae (Sauvage 1897–1898, pl. 7, figs. 2–6) may be iguanodontid but the material is generically and specifically indeterminate. It should be noted that the material figured by Sauvage (1897–1898, pl. 7, figs. 2–12) was destroyed in World War II.

Sauvage (1897–1898, pl. 7, fig. 1) also referred two associated sacral centra (Geological Service of Portugal Collections) from the Kimmeridgian of Porto-de-Mós (Leira), Portugal, to *I. prestwichii*. However, Lapparent and Zbyszewski (1957, p. 51) note that the vertebrae are those of a juvenile plated dinosaur (*Dacentrurus* (= *Omosaurus*) *lenneri*).

von Huene and Maubeuge (1954) described a partial camptosaurid pubis from the Upper Jurassic (Rauracien) of Fours à Chaux d'Haudainville, near Verdun, France. The anterior process is much more dorso-ventrally expanded and plate-like with more divergence between the dorsal and ventral edges than there is in *Camptosaurus* (text-fig. 2C, D). The expanded form of the anterior process is more similar to that of *Ouranosaurus* and the robust form of *Iguanodon* (see Dollo 1882*a*; Casier 1960). This pubis is identified as iguanodontid, generically and specifically indeterminate.

4. *Camptosaurus leedsi* Lydekker (1889) is based on a left femur (text-fig. 2G) from the Oxford Clay that was referred to the Oxfordian (Upper Jurassic) by Galton (1975). However, Hoffstetter (1957) noted that the bone-bearing layer is the lower Oxford Clay, which is of Upper Callovian (Middle Jurassic) age. This femur differs from that of *Camptosaurus* (text-fig. 2F–H) in several respects: the greater trochanter is much less massive, the fourth trochanter is more proximally placed, distally the anterior surface does not sweep out to form a wider anterior end and the anterior intercondylar groove is much more shallow. This femur should not be referred to the genus *Camptosaurus* and it probably represents a new genus.

SYSTEMATIC PALAEONTOLOGY

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family IGUANODONTIDAE
Camptosaurus MARSH, 1885

Type species. Camptonotus dispar Marsh, 1879, p. 501.

Type locality. Quarry 13 near Como Bluff, Albany County, Wyoming, U.S.A.

Known distribution. Upper Jurassic of western U.S.A. and England; Lower Cretaceous of western U.S.A.

Diagnosis. Skull low and wide, large posterior process to premaxilla, small antorbital fenestra, small contribution of frontal to orbital margin, surpaoccipital borders foramen magnum, premaxilla edentulous, fifteen or sixteen functional teeth in each maxilla and dentary, and one replacement tooth per alveolus; teeth lozenge-shaped with prominent vertical keel more strongly developed on maxillary teeth than on dentary teeth, several secondary vertical ridges on sculptured surface of crown with anterior and posterior ridges bordering the non-deniculate half of maxillary tooth crown, posterior ridge on equivalent part of dentary teeth. Nine cervicals, sixteen dorsals, and six or seven sacral vertebrae; cervicals 4–9 opisthocoelous; variable development of peg-and-notch articulation between sacral centra. Scapula longer than humerus, which has a poorly developed deltopectoral crest. Deep ilium with long anterior process and narrow brevis shelf. Pubis with a deep evenly expanded anterior process and elongate posterior process that reaches end of ischium. Ischium with proximally placed obturator process and bar-shaped distal part with dorso-ventrally expanded end. Femur curved, longer than tibia with pendant fourth trochanter extending on to distal half of shaft and distally a well-developed anterior intercondylar groove. Pes robust with four digits, first being rudimentary. The width is greater than the length in phalanges 3 and 4 of digit IV of pes.

Camptosaurus dispar (Marsh)

1879 *Camptonotus dispar* Marsh, p. 501, pl. 3.
1879 *Camptonotus amplus* Marsh, p. 503.
1885 *Camptosaurus dispar* (Marsh), Marsh, p. 169.
1885 *Camptosaurus amplus* (Marsh), Marsh, p. 169.
1894 *Camptosaurus medius* Marsh, p. 85.
1894 *Camptosaurus nanus* Marsh, p. 85, pl. 5, fig. 3.
1909 *Camptosaurus browni* Gilmore, pp. 230–297.

Type species. Camptonotus dispar Marsh, 1879, p. 501, pl. 3.

Type specimens. Holotype YPM 1877 (partial skeleton), paratypes YPM 1877a (partial sacrum), YPM 1878 (pelvic girdle and forelimb).

Type locality and horizon. Morrison Formation (Upper Jurassic, Upper Kimmeridgian ≡ Lower Tithonian) of Quarry 13 near Como, Albany County, Wyoming, U.S.A.

Known distribution. Upper Jurassic of Wyoming, Utah, and Colorado.

Diagnosis. Large intramaxillary cavity, posterior process of premaxilla reaches prefrontal, three or four secondary ridges reach middle of tooth crown anterior to prominent keel. Centrum of cervical three platycoelous, ventral edge of anterior end of cervical centra four to nine gently rounded. Well ossified carpus, radiale and metacarpal I fused, five short and stocky digits. Massive long bones and pes.

Camptosaurus prestwichii (Hulke)

1880 *Iguanodon prestwichii* Hulke, pp. 433–456, pls. 18–20.
1888 *Cumnoria prestwichii* (Hulke), Seeley, p. 698.
1889 *Camptosaurus prestwichii* (Hulke), Lydekker, p. 259.

Type species. Iguanodon prestwichii Hulke, 1880, p. 433.

Holotype. OUM J.3303 (almost complete skeleton).

Type locality and horizon. Lower Kimmeridge Clay (upper Lower Kimmeridgian *Aulacostephanus pseudomutabilis* Zone, Upper Jurassic), Chawley Brick Pit, Hurst Hill, Cumnor, 2·5 miles WSW. of the centre of Oxford, England (National Grid reference SP 475 043).

Known distribution. Upper Jurassic of England.

Diagnosis. Small intramaxillary cavity, five secondary ridges reach middle of tooth crown anterior to prominent keel. Anterior end of cervical centra 4–9 subrhomboidal in outline. Slender long bones and pes.

Camptosaurus depressus Gilmore

Type species. Camptosaurus depressus Gilmore, 1909.

Holotype. USNM 4753 (partial skeleton).

Type locality and horizon. 'Calico Canyon' near Buffalo Gap Station, South Dakota, from Lakota Sandstone (Lower Cretaceous, ?Aptian).

Diagnosis. Ilium low with shallow acetabulum and narrow preacetabular notch. Sacrals with rounded ventral surfaces. Anterior end of pubis broad. (The validity of this species is provisionally accepted, but the type material needs to be fully described.)

PALAEOBIOGEOGRAPHICAL IMPLICATIONS

The similarities between the dinosaurian faunas of the Morrison Formation of the western interior of North America and the Tendaguru Beds of Tanzania, East Africa, can be accounted for only by assuming the presence of a land connection between the two areas some time during the Late Jurassic (Galton 1977*a*, *b*). Western Europe and North America are presumed to have been connected at this time (Charig 1973; Colbert 1974; Cox 1974) but faunal evidence for this is slight.

The Morrison stegosaur *Stegosaurus* was reported from the Oxford Clay (Upper Callovian, Middle Jurassic) from near Peterborough, England, but *Stegosaurus priscus* Nopcsa, 1911 is regarded by Hoffstetter (1957) as a juvenile of *Omosaurus durobrivensis* Hulke, 1887, the type species of the genus *Lexovisaurus* Hoffstetter, 1957. Lydekker (1890*a*) referred *Omosaurus armatus* Owen, 1875 from the Kimmeridge Clay of Swindon to *Stegosaurus* but Lucas (1902) subsequently made it the type species of the genus *Dacentrurus*. Both *Lexovisaurus* and *Dacentrurus* differ in many respects from the

Morrison *Stegosaurus* (see Hoffstetter 1957; Steel 1969). Galton (1976*c*) referred the Morrison theropod dinosaur *Stokesosaurus clevelandi* Madsen, 1974 to the Middle Jurassic English genus *Iliosuchus* von Huene, 1932 but this was incorrect (Galton and Jensen 1979*b*). *Apatosaurus* and *Brachiosaurus*, two genera of Morrison sauropods, are described from the Kimmeridgian of Portugal by Lapparent and Zbyszewski (1957), but these generic referrals are probably incorrect (J. S. McIntosh, pers. comm.). *Cteniogenys antiquus* Gilmore, 1928 is the only Morrison lizard known and Seiffert (1973) described a new species, *C. reedi* from the Lower Kimmeridgian of Portugal. However, only upper and lower jaws are available for comparison and these are very similar to those of *Kuehneosaurus* Robinson, 1962 from the Upper Triassic of England (Estes, in press).

From the above review, it is apparent that there is little faunal evidence for a land route between the western interior of North America and western Europe during the late Middle or early Late Jurassic. This situation is rectified to a certain extent by the description given above of the reasonably complete skeleton from England that is referred to the Morrison genus *Camptosaurus* as *C. prestwichii* (Hulke). However, the land route was probably available for a relatively short period of time, because the maximum extent of Jurassic seas was reached during the Callovian, Oxfordian, and Kimmeridgian, when between a quarter and a third of the total continental area was covered (Hallam 1969, 1975). The continental area showing most submergence was western Europe and northern Africa and, because of this, it was suggested (Galton 1977*a*, *b*) that the Morrison–Tendaguru connection was probably via Central and South America rather than via Europe as commonly assumed (Charig 1973; Colbert 1974; Cox 1974).

Two genera of ornithopod dinosaurs from the Morrison Formation (Upper Kimmeridgian, about 138 m.y. van Hinte 1976) of the western interior of North America have an intercontinental distribution: *Camptosaurus* and *Dryosaurus*. The anatomy of *Camptosaurus prestwichii* from the Lower Kimmeridgian (about 141 m.y. van Hinte 1976) of England differs in several respects from that of the slightly more recent *C. dispar* (text-fig. 2; table 3). This is not the result of a growth difference, because the limb bones of *C. prestwichii* are proportionately more slender than those of the smaller individual (humerus length 143 mm *v.* 297 mm) of *C. dispar* illustrated by Gilmore (1909, 1912) as *C. nanus*. The difference in build probably represents a relatively short-term evolutionary change because both a gracile and a massive species of *Iguanodon* lived together in the Early Cretaceous of western Europe (Casier 1960). The difference in the sacral centra may represent evolutionary divergence resulting from the more recent occurrence of the Morrison species. However, the reduction in size of the intramaxillary cavity, with additional ossification lateral to the tooth row, is an advanced character for an ornithopod (see Galton 1974*a*). Consequently, it is surprising that this reduction occurs in *C. prestwichii* rather than in the more recent *C. dispar*. The anatomy of the Morrison hypsilophodontid *Dryosaurus altus* is extremely similar to that of *D. lettowvorbecki* from the Tendaguru Beds (Upper Kimmeridgian) of Tanzania, East Africa (Galton 1977*a*, *b*).

The higher degree of evolutionary divergence of the two species of *Camptosaurus* is probably not a function of distance, because their Upper Jurassic positions are only half as far apart as were those of *Dryosaurus* (see maps in Cox 1974; Galton 1977*a*, *b*; Hallam 1977), but it may be that the two species of *Camptosaurus* were isolated from each other for a longer period of time than was the case for the species of *Dryosaurus*. The North Atlantic epicontinental seaway was a barrier to gene flow for *Camptosaurus*; on the basis of evidence from marine molluscs, this was established by the Pliensbachian (183 m.y.) at the latest and persisted throughout the Jurassic (Hallam 1977). If the Morrison–Tendaguru connection was via South America, then the Central Atlantic, linking the Pacific to Tethys, was a barrier for *Dryosaurus*. Hallam (1977) notes that the Central Atlantic was probably represented in the latest Aalenian and early Bajocian by a well-developed epicontinental seaway which later became restricted or intermittently closed until the Mid Callovian, but that true oceanic crust was not created in the Central Atlantic, by the movement apart of North America and South America plus Africa, until late Callovian or, more definitely, Oxfordian times (149 m.y.). It is apparent that the excessively long times involved (40 m.y. for *Camptosaurus*, 10 m.y. for *Dryosaurus*) indicate that the dispersal of these genera did not occur prior to the origin of the seaways. A land route across the North Atlantic epicontinental seaway was probably available for the dispersal of *Camptosaurus* some time in the Oxfordian (144 m.y.) and for *Dryosaurus* across the western end of the Central Atlantic some time in the Kimmeridgian.

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Note added in press. The results of additional research by the senior author are relevant to some of the contents of this paper. A 366-mm long femur from the Geological Survey of Portugal Collections, very similar to those of *Camptosaurus dispar*, is described from the Kimmeridgian of Portugal (Galton, in press *a*, *b*). The holotype femur of *Camptosaurus leedsi* (p. 437) is redescribed and made the type specimen of a new ornithopod genus (Galton, in press *b*). The holotype femur of *Cryptodraco eumerus* (pp. 428, 433) is also redescribed (Galton, in press *b*); because of its close similarity to the femur of the nodosaurid ankylosaur *Hoplitosaurus marshii* (Gilmore 1914), *Cryptodraco* is transferred to the ankylosaurian family. Nodosauridae (Galton, in press *b*, *c*). *Priodontognathus phillipsii* (pp. 413, 420, 433) is also transferred to the Nodosauridae because the teeth are similar to those of the nodosaurid *Sauropelta edwardsi* Ostrom, 1970 (Galton, in press *c*).

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THE ROLE OF BODY EXTENSION IN CEPHALOPOD LOCOMOTION

by JOHN A. CHAMBERLAIN, JR

ABSTRACT. The extension of the body outward from the aperture of the shell is a common behavioural trait of *Nautilus*, and presumably of most fossil ectocochliate cephalopods as well. In order to evaluate the possible contribution of body extension to ectocochliate locomotion, the hydrodynamic properties of body extension have been examined through tow-tank and flow-channel tests on shell models and body prostheses. Extension of the body reduces the drag generated by a swimming cephalopod. The extent of this reduction depends on how fully the body is extended, and on its posture relative to the flow. For most cephalopods this effect was probably small, but for some with compressed shells, and perhaps for *Nautilus*, an energy saving in the order of 25% may have been attainable. Extension of tentacles into the flow causes serious drag increases and can quickly overcome the beneficial effects of body extension. To minimize its drag, *Nautilus* retracts its tentacles when swimming fast, and in this aspect of its locomotory behaviour mirrors fish and squids, which do the same thing with their fins.

THE drag produced by a swimming animal depends not only on its general body shape, but also on details of its external anatomy. In the case of fossil cephalopods, a number of aspects of morphology besides basic shell geometry can be cited as possible contributors to drag production, and thus may be important in the locomotion of these animals. One of these factors is the extension of the body of the animal outward (backward actually) from the aperture. As it extends itself, an ammonoid or nautiloid can more readily interact with the flow and perhaps alter flow patterns around itself in a way that has some bearing on its progress through the water.

The significance of this kind of phenomenon has been of some interest to cephalopod palaeontologists in their attempt to understand the locomotory capacity and life styles of these animals. Schmidt (1930), who was the first student of cephalopods to develop quantitative data on shell flow properties, believed that body extension was undoubtedly an important hydraulic factor, and as a result was not confident that his drag measurements for empty shells were completely representative of the drag produced by the living animal. Geczy (1960) extended this notion by asserting that body extension was more important in drag production than many modifications of the shell. By drawing an analogy between the extended body of a cephalopod and the afterbodies of aircraft gun barrels, I have argued that body extension was probably not an important hydrodynamic factor for most shell forms (Chamberlain 1976). My main point was that in order to reduce drag significantly, afterbodies had to be about the same size as the barrel itself. I reasoned that the size of the extended body had to have been about the same as that of the shell and that the body should have extended forward into the umbilicus in order to produce a significant drag reduction in cephalopods. This clearly could not have occurred for most fossil cephalopods because evidence from buoyancy considerations, colour markings, pre-mortal epizoans, and general anatomy oppose this view.

While the gun-barrel analogy seems a cogent one, no hydrodynamic data exist that actually establish the hydraulic significance of body extension. The purpose of the present work is to fill this void. This paper reports results of experiments involving the use of plastic cephalopod shell models and wooden 'body' prostheses. These experiments are designed to develop data on flow patterns and drag coefficients of the shell and extended body. The work is directed toward resolving the question of the effectiveness of body extension in reducing the total drag acting on the animal, which I see as the crux of the debate on body extension. Other locomotory functions that may benefit from body extension, such as equilibrium and directional control, and such non-hydrodynamic functions as grasping, food capture, and visual enhancement, are not dealt with directly here.

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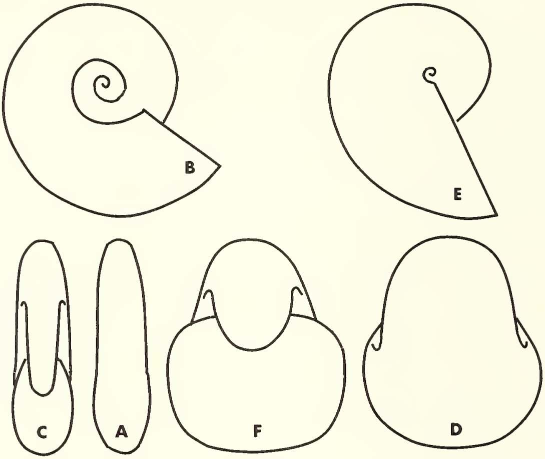
METHODS

The approach employed here is based on the experimental procedures that I developed previously for studying the hydrodynamic properties of cephalopod shells (Chamberlain 1976). The procedure consists of two parts: (1) construction of shell models and body prostheses; and (2) testing the models in a tow tank and water channel.

I built two shell models using the template method of model construction described in Chamberlain (1969). One model has a compressed, moderately evolute form, while the other is depressed and involute (see text-fig. 1). Table 1 gives the dimensions of the two models and values for the descriptive parameters used to characterize the



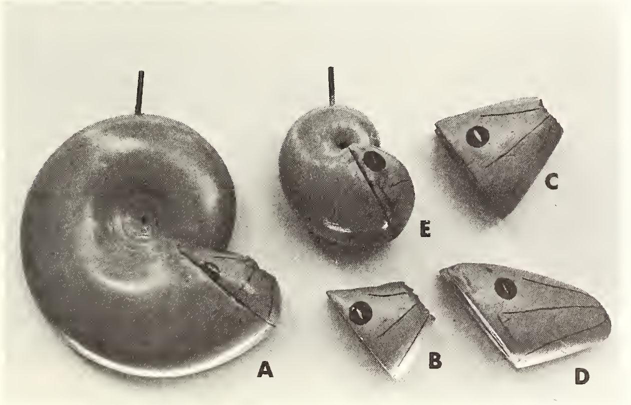
TEXT-FIG. 1. Plastic shell models used in this study. *A*, *B*, *C*: anterior, lateral, and posterior views of compressed model (model C). *D*, *E*, *F*: anterior, lateral, and posterior views of depressed model (model D). The terms anterior and posterior refer to orientation relative to the direction of motion of the swimming animal. No anatomical significance to these terms should be inferred.

TABLE 1. Geometrical parameters for shell models used in experiments. *W*, expansion rate; *D*, relative distance of whorls to the coiling axis; *S*, shape of whorl section; *F*, relative position of maximum whorl width. For algebraic definitions of geometrical parameters see Raup (1967) and Chamberlain (1976). Fineness ratio = maximum width of shell/shell diameter.

	General shape	Maximum diameter (cm)	Aperture width (cm)	Aperture height (cm)	Fineness ratio	Geometrical parameters			
						W	*D*	*S*	*F*
Model C	Compressed, moderately evolute	25·4	6·5	11·5	0·26	2·0	0·2	0·5	0·25
Model D	Depressed involute	12·7	10·5	8·5	0·83	3·5	0·07	1·25	0·4

geometry of coiled shells (see Raup 1967; Raup and Chamberlain 1967; Chamberlain 1976). The models were sanded and varnished to produce a smooth, mirror-like surface.

Extension of the body backward from the aperture was simulated by attaching realistically shaped body prostheses to the aperture of the shell models. Four such prostheses were fashioned from balsa-wood blocks for testing with the compressed model (model C), and one for testing with the depressed model (model D). Text-fig. 2 shows these prostheses. Except for the rear surface, which was left rough in three of the prostheses to simulate the irregularities made by the tips of the tentacles, each prosthesis was sanded and varnished to give it a smooth surface. In a general way, the shape of these prostheses is similar to the extended body of *Nautilus*, as shown in text-fig. 3. Each conforms to the whorl section of the shell model for which it is designed, and then tapers posteriorly. The prostheses differ from one another in size, degree of taper, and orientation relative to flow (see Table 2, text-fig. 2). However, the prostheses, being rigid, do not reproduce the elasticity of the skin in *Nautilus*, and thus would not be helpful in evaluating the possible damping effects of the skin on boundary-layer vorticity.



TEXT-FIG. 2. Body prostheses in lateral view. *A*: model C with small prosthesis (P1) attached to aperture. *B*: medium prosthesis (P2). *C*: large prosthesis (P3). *D*: streamlined prosthesis (P4). Prostheses 1–4 for use with model C. *E*: model D with prosthesis P5 attached to aperture.

TABLE 2. Dimensions of body prostheses. Prosthesis *P*1–*P*4 for use with compressed model; prosthesis *P*5 for use with depressed model. Length = length in cm along midline of prosthesis. Relative size = prosthesis length/maximum shell diameter. Taper = $\frac{1}{2}$ (width of aperture − width at rear of prosthesis)/length. Orientation relative to flow = angle in degrees between midline of prosthesis when attached to shell model and the direction of water flow around shell.

Body Prosthesis	length	Relative size	Taper	Orientation relative to flow
P1	4·5	0·18	0·28	45
P2	6·0	0·24	0·21	45
P3	9·0	0·35	0·17	45
P4	12·0	0·47	0·21	20
P5	3·0	0·24	1·08	30

TEXT-FIG. 3. Live specimen of *Nautilus pompilius* swimming in its tank at the New York City Aquarium. Degree of body extension shown here is equivalent to that of body prostheses.

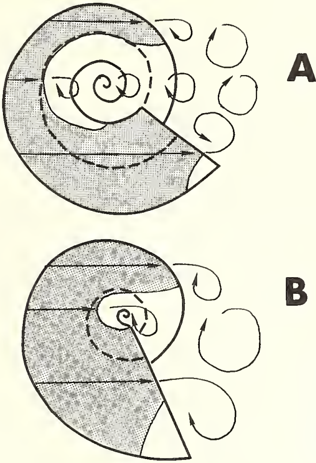
Shell flow patterns were visualized by cementing dye crystals to the models and immersing them in a flow channel. Drag coefficients were determined from drag and velocity data obtained by testing the models in a tow tank (see Chamberlain 1976 for a more complete description of these procedures). The tests were performed with the flow channel and tow tank at Webb Institute of Naval Architecture, Glen Cove, N.Y.

The flow-channel and tow-tank tests were done using velocities likely to have been attained by fossil cephalopods. Analogy with *Nautilus* and other modern swimmers (Chamberlain and Westermann 1976) suggests the appropriate velocity range as 0–120 cm/sec, with most interest centring on the lower end of the range. The flow-channel tests were conducted at velocities of 30 cm/sec and 60 cm/sec; while the tow-tank tests covered a range of 35–110 cm/sec by making about twenty constant-velocity runs at small intervals within these extremes for each model configuration studied. Since the tow-tank carriage was designed for the high speeds of interest to naval architects and engineers, velocities lower than 35 cm/sec could not be attained with the apparatus used here.

To establish a basis for evaluating the hydrodynamic effects of body extension, the two shell models were first tested without body prostheses. Then prostheses were attached to the models and the tests repeated for each model-prosthesis configuration of interest. This procedure was followed in both tow-tank and water-channel experiments.

FLOW PATTERNS OF SHELL MODELS

The sketches in text-fig. 4, which are composites based on visual observation and photographs, show the flow field around each model. In each case the boundary layer remains attached to the surface of the model over the leading portion of the outer whorl, and then separates along the umbilical shoulder and the periphery of the aperture. Separation of the shell boundary layer at these locations induces a turbulent wake of considerable magnitude behind the shell. These results are consistent with my earlier determinations of cephalopod flow structure (Chamberlain 1976).

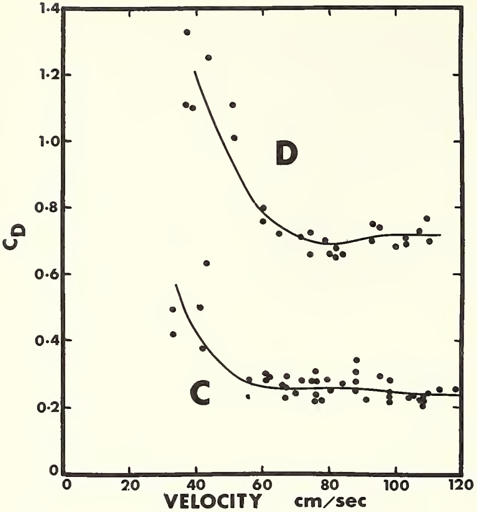


TEXT-FIG. 4. Flow fields of shell models without body prostheses. *A*: model C. *B*: model D. Area of boundary-layer attachment shown by stippling. Flow streamlines shown by solid lines. Umbilical shoulder shown by dashed line on outer whorl.

DRAG OF SHELL MODELS

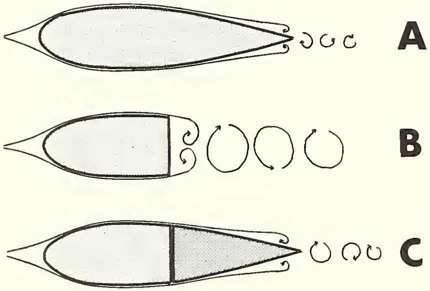
Text-fig. 5 shows the results of the tow-tank tests plotted as drag coefficient (C_D) against velocity. Although drag coefficient is consistently lower for the compressed model, both models show the same kind of inverse relationship between drag coefficient and velocity. Two aspects of this relationship are worth noting: (1) drag coefficent diminishes rapidly as velocity increases at velocities below about 50 cm/sec; and (2) drag coefficient levels off and becomes nearly independent of velocity above about 50 cm/sec.

Drag-coefficient changes of the magnitude observed at low velocity in text-fig. 5 often occur when the position of boundary-layer separation shifts along the surface of an object. Fisher (1977), for example, observed this effect in the flow dynamics of the Pennsylvanian xiphosurian *Euproops danae*. In the present case, however, the reduction in drag coefficient occurs at Reynolds numbers ($Re \approx 2 \times 10^4$) for which this phenomenon would not normally be expected, and probably reflects nothing more substantial than the fact that the drag forces produced at these low velocities approximate the sensitivity of the dynemometer used to measure drag. The validity of these high drag coefficients at low velocity is thus suspect.



TEXT-FIG. 5. Drag coefficient (C_D) of shell models without body prostheses as a function of velocity. *C*, model C. *D*, model D. Each dot represents one constant-velocity tow-tank run. Curves fit by eye.

Above about 50 cm/sec, where drag forces are sufficiently large to be recorded accurately by the dynemometer, the drag coefficient—velocity curves in text-fig. 5 assume the flattened form typical of blunt, rounded bodies at Reynolds numbers of 10^4–10^5, and of the shell-drag coefficient curves that I obtained in previous experiments (Chamberlain 1976; text-fig. 6). Since model drag coefficients are virtually constant above 50 cm/sec, I calculated an average drag coefficient for each model. These average drag coefficients are given in Table 3. I would emphasize that, strictly speaking, the average values apply only to the velocity range of 50–110 cm/sec, although good hydrodynamic arguments exist for believing that the drag coefficient values given in Table 3 extend beyond these limits as well.



TEXT-FIG. 6. Flow fields around three bodies. *A*: fully developed fusiform body. Boundary layer remains attached to surface for considerable distance behind leading edge. Small wake. Low drag. *B*: underdeveloped body. Boundary layer is forced to separate prematurely at trailing edge. Wake large. High drag. *C*: underdeveloped body and afterbody. Boundary layer does not separate from trailing edge of leading body but remains attached over much of afterbody. Flow takes on characteristics of that for fully developed body.

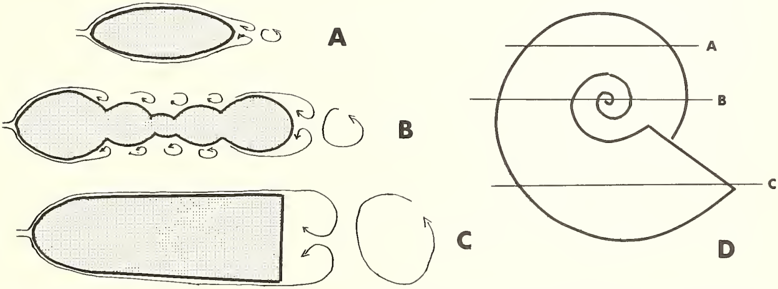
TABLE 3. Average drag coefficients of smooth surfaced shell models. N, number of tow-tank runs; C_D, drag coefficient.

	Average		
	N	C_D	Std. Dev.
Model C	45	0·26	0·035
Model D	23	0·71	0·038

The probable swimming velocities of real animals the size of the models probably lie within the range to which the average drag coefficients most strictly apply (Chamberlain and Westermann 1976; text-fig. 7).

The marked difference in the drag coefficients of the two models noted in Table 3 is the result of difference in morphology, especially with respect to S (see Table 1). Because it is compressed (low S), model C has a smaller frontal area (projected area in direction of flow) relative to its size than does model D (compare text-fig. 1A and D). Thus, model C intercepts and redirects relatively less water than model D, and hence generates less drag. Model C also has a smaller aperture relative to its size than does model D—a feature which likewise derives from its compressed form (compare text-fig. 1C and F). Consequently, premature boundary-layer separation along the periphery of the aperture, and the drag elicited by this forced separation, is therefore less in model C. The hydrodynamic advantage gained by model D in having a small umbilicus is apparently overshadowed by the effects of these S-related aspects of shell geometry. This result is consistent with my previous findings concerning the relative contributions of W-, S-, and D-related drag components to total shell drag (Chamberlain 1976).

Table 4 compares models C and D with shell models of similar morphology tested previously. For model C and model 10, which differ mainly in the degree of shell compression (S), drag coefficient is seen to be much lower in the compressed specimen. The same relation is also seen in the data for the second group of specimens listed in Table 4, where the chief morphological variable is again shell compression. Drag-coefficient differences between specimens having the same compression (models 5 and 10) are due to differences in the degree of inflation (W). Model 5 has a somewhat higher drag



TEXT-FIG. 7. Flow over different parts of a cephalopod shell. *A*: flow across top of shell. *B*: flow in umbilicus. *C*: flow around bottom of shell and aperture. Flow is fully developed in *A*. Underdeveloped in *B* and *C*. *D*: lateral view of shell showing locations of cross-sections *A–C*. After text-fig. 5 of Chamberlain (1976).

TABLE 4. Average drag coefficients of smooth-surfaced specimens. Data for model 5, model 10, and *Nautilus pompilius* from Chamberlain (1976).

	Average	Shell geometry			
	C_D	W	D	S	F
Model 10	0·57	2·0	0·2	1·0	0·23
Model C	0·26	2·0	0·2	0·5	0·25
Model D	0·71	3·5	0·07	1·25	0·4
Model 5	0·63	3·5	0·1	1·0	0·29
Nautilus pompilius	0·48	3·25	0·05	0·7	0·57

coefficient than model 10 because, being slightly more inflated, it has a relatively large frontal area and aperture. These results support my earlier assertion (Chamberlain 1976) that the shell morphology exhibiting the lowest over-all drag is probably one characterized by the smallest possible compression, inflation, and umbilicus (low S, low W, low D).

EFFECT OF BODY EXTENSION

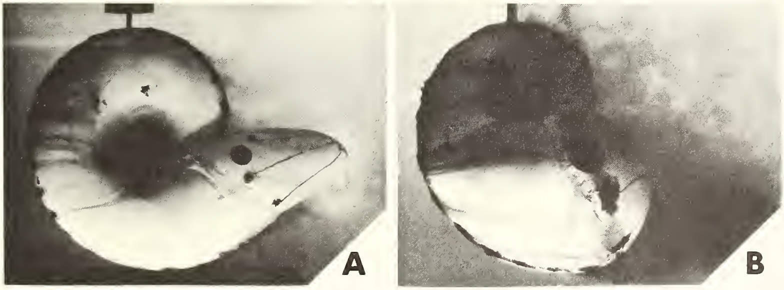
The gentle curvature found in elongate, fusiform (fully developed) bodies allows the boundary layer to flow across the surface of the body with a minimal rate of momentum loss. As a result, the boundary layer remains attached to the surface for a considerable distance behind the leading edge of the object, thus ensuring that when the boundary layer does separate, the ensuing turbulence and drag are also minimal (text-fig. 6A). In contrast, the abrupt change in curvature of an underdeveloped body (text-fig. 6B) forces the boundary layer to separate before it would otherwise do so. This premature separation creates much turbulence and hence produces high drag forces. This situation can be greatly ameliorated by appending a second object, or afterbody, to the rear of the underdeveloped body (text-fig. 6C). If the afterbody is properly designed, i.e. if it is large enough to fill the dead-water region behind the first object and if it continues the curvature with no sharp gaps, the flow will be largely restored to the low turbulence, low drag condition of the fully developed body (text-fig. 6C).

A cephalopod shell is morphologically more complex than the simple bodies illustrated in text-fig. 6, but it nevertheless consists of regions that can be considered as fully developed or underdeveloped. In text-fig. 7, for example, it is clear that the upper part of the shell (text-fig. 7A) acts like a fully developed body. The gentle curvature of this part of the shell encourages the boundary layer to remain attached to the shell surface for some distance behind the leading edge (venter). However, the inward curve of the umbilical shoulder (text-fig. 7B), and especially the truncation at the aperture (text-fig. 7C) cause the boundary layer to separate prematurely from the rest of the shell. As a result of most of the shell being effectively underdeveloped, the drag on a cephalopod shell is relatively high.

The underdevelopedness of a cephalopod shell can be minimized through such modifications of shell geometry as reduction in the size of the umbilicus and aperture relative to the size of the shell (Chamberlain 1976). Another means to the same end would obviously be to extend the body backward from the aperture. If done properly, body extension could eliminate boundary-layer separation along the peristome and reduce the size of the stagnant region behind the shell, in the same way as for the afterbody illustrated in text-fig. 6C. Behaviour of this kind might be particularly important in those species where the details of shell form are specified by adaptive requirements other than drag minimization—a condition that may indeed be the general one because relatively few species appear to have shells close to the ideal for drag minimization.

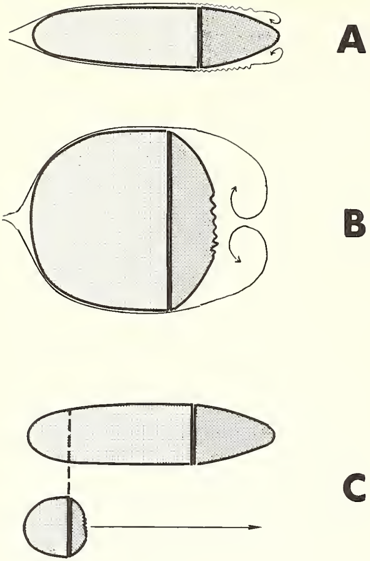
FLOW PATTERNS OF SHELL MODELS AND BODY PROSTHESES

Text-fig. 8 shows the flow field set up by the shell models with attached body prosthesis. Comparison of text-fig. 8 with text-figs. 4 and 7 (see also text-fig. 4, and pl. 84 of Chamberlain 1976) demonstrates that the structure of the flow is essentially the same for both the shell alone and the shell with body. In both cases the flow separates along the umbilical shoulder of the models (shown in text-fig. 8 by distortion of dye streams on the flank of the outer whorl), and both elicit a wake of considerable magnitude (shown in text-fig. 8 by swirls of dye behind shell and in umbilicus). However, it is also clear from text-fig. 8 that the body prostheses do in fact act like the afterbody illustrated in text-fig. 6c. This is most readily apparent in text-fig. 8A where the dye streams emanating from the clusters of dye crystals on the body prosthesis are seen to streak out backward along the surface of the prosthesis. Premature boundary-layer separation at the aperture does not occur. Instead the boundary layer remains attached over most of the prosthesis. Note, however, that in contrast to the narrow, laminar streamlines at the leading edge of the shell, the dye streams on the prosthesis are wide, and evidently turbulent. Apparently by the time the boundary has reached the flank and rear of the prosthesis it has become turbulent and is ready to separate.



TEXT-FIG. 8. Flow fields of models with body prostheses attached to aperture. Flow velocity = 30 cm/sec. *A*: model C + prosthesis P4. *B*: model D + prosthesis P5. Dark objects along the venter, flank of the outer whorl, and on the side of the body prostheses are clusters of dye crystals.

In text-fig. 8B the afterbody effect is less obvious, although prosthesis P5 does fill a large volume behind model D. The dye released by the crystal clusters on prosthesis P5 appear to spread parallel to the peristome rather than backward as would be expected if flow were attached. Thus, it would appear that the boundary layer has already separated from the surface of the model despite the presence of the prosthesis. Evidently the major effect of the prosthesis in this case is to limit the scale of wake turbulence rather than to seriously modify boundary-layer behaviour. The difference between the two models in this respect undoubtedly derives from the differences between them in surface curvature. As suggested in text-fig. 9, attachment of the boundary layer in the case of model C is promoted by addition of the prosthesis because it continues the curvature of the model (text-fig. 9A). In contrast, prosthesis P5 (text-fig. 9B) does not continue the curvature of model D, but greatly magnifies it. As for the umbilical shoulder, momentum loss resulting from this rapid change in curvature is apparently severe enough to cause the boundary layer to stall and then separate at this location.



TEXT-FIG. 9. Flow patterns in region of aperture for shell models with prostheses. *A*: model C+prosthesis P4. Boundary layer is laminar at first and then develops vortices over the prosthesis. *B*: model D+prosthesis P5. Boundary layer separates due to curvature change at model-prosthesis juncture. Orientation of these cross-sections is the same as in text-fig. 7C. *C*: cross-sections drawn to same scale to emphasize that in terms of its flow properties, a depressed shell is equivalent to the anterior portion of a compressed shell, and that to produce a fully developed form, an animal with a depressed shell must extend its body much more than one with a compressed shell.

DRAG OF SHELL MODELS AND BODY PROSTHESES

Plots of drag coefficient against velocity for all model-prosthesis configuration tests give the same results as described above for the models alone, namely, drag coefficient is nearly independent at all but the lowest velocities attained with the test apparatus. Hence, I calculated drag coefficients for each model-prosthesis combination (Table 5). As in the case of the shell models alone, these drag coefficients should be considered as applying to the velocity range of about 50–110 cm/sec, but probably are valid for some distance beyond these limits also.

It seems clear from Table 5 that the addition of the prostheses to the shell models reduces drag coefficient. In view of the relatively minor differences between some test configurations, however, I performed *t*-tests on the data to determine if the observed differences are statistically meaningful. The results of these calculations are given in Table 6. It will be noted that some of the drag-coefficient differences are not statistically significant.

The data given in Tables 5 and 6 suggest some general rules about the functioning of body extension in ectocochliate locomotive hydrodynamics. The most obvious effect is to reduce the drag coefficient of the animal, and thus to enhance its hydrodynamic efficiency. In practical terms, this enhancement can be in the form of increasing velocity by the same relative amount that the drag coefficient is reduced, assuming that the energy saved is put back into the propulsive system. Alternatively, it can take the form of reducing propulsive output required to attain a given velocity with the concomitant saving of energy going to increase the animal's locomotory stamina, or into its general energy reserve.

TABLE 5. Average drag coefficients of shell models and body prostheses. *N*, number of tow-tank runs; C_D, drag coefficient. $\%C_D$ decrease $= 100 \times [(C_D$ of shell model$) - (C_D$ of shell model + prosthesis$)]/(C_D$ of shell model$)$. Fineness ratio at aperture = fineness ratio of apertural region of shell = maximum shell width/[(projected distance from venter to aperture in direction of flow) + length of body prosthesis, if present)]. A fully developed body has a fineness ratio = 0·20–0·24; underdeveloped body (too short) > 0·30. Overdeveloped body (too long) < 0·20.

Test configuration	*N*	Average C_D	Std. Dev.	$\% C_D$ Decrease	Fineness ratio at aperture
Model C	45	0·26	0·035	—	0·30
Model C+P1	20	0·22	0·018	15	0·28
Model C+P2	18	0·23	0·041	12	0·27
Model C+P3	17	0·24	0·025	8	0·24
Model C+P4	21	0·20	0·077	23	0·22
Model D	23	0·71	0·038	—	1·40
Model D+P5	18	0·64	0·083	10	1·00

The extent to which drag coefficient is reduced appears to be relatively small (about 10%) in most of the examples studied. Thus, the beneficial contribution of body extension to over-all locomotive capacity is likewise probably of minor consequence to the animal. This is to be expected in view of the fact that body extension in ectocochliates does not achieve a fully developed state for the shell-animal combination. The extended body does not completely fill the stagnant region behind the shell (text-fig. 8); it does not project into the umbilicus to prevent separation along the umbilical shoulder; nor does it necessarily inhibit separation at the peristome (text-fig. 8B). Despite these shortcomings of ectocochliate adaptive design, the data for model C+P4, where drag coefficient is reduced by 23% from the shell model alone, suggest that some ectocochliates may have been able to generate useful reductions in drag. As in the case of model C, those animals most likely to have done so, would have compressed shells because compressed shells have lower fineness ratios (see Table 1) and thus are more fully developed without body extension, and more likely to be fully developed when the body is extended (see text-fig. 9C; Table 5, column 6). As I have suggested previously (Chamberlain 1976), this would be especially true in high-shouldered oxycones because in such shells umbilical drag is small; the drag produced at the aperture is the major component of total shell drag. Reducing aperture drag by extending the body in these shells will therefore produce a much larger reduction in total drag than in the case of model C where, judging from its flow structure (text-fig. 8A), the umbilicus is a major drag contributor.

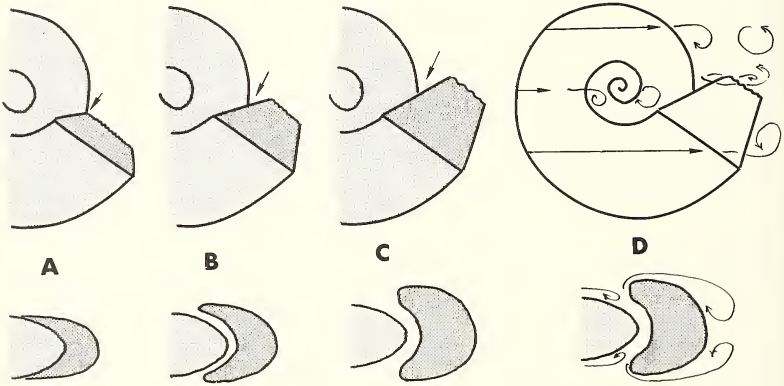
TABLE 6. Results of *t*-tests for determining significance of average C_D for the various test configurations studied. *, average C_D different at 95% confidence level; 0, average C_D not different at 95% confidence level.

	Model C + P1	Model C + P2	Model C + P3	Model C + P4	Model D + P5
Model C	*	*	0	*	
Model C+P1		0	*	0	
Model C+P2			0	*	
Model C+P3				*	
Model D					*

In principle, one would expect the magnitude of drag reduction to reflect the degree to which the body is extended. A protrusive body should produce a more fully developed form in the apertural region of a shell than a retracted body exposing only the tips of the tentacles. Yet, the data do not appear at first glance to support this expectation. Prostheses P1 through P4, while increasing uniformly in size relative to the shell (Table 2, column 2) and thus producing a progressively more fully developed form (Table 5, column 6), do not produce a correspondingly progressive reduction in drag coefficient (Table 5, column 5). P3, for example, elicits only an 8% drag-coefficient decrease (which is not statistically significant), whereas P1, which is much smaller than P3, gives a reduction nearly twice as large.

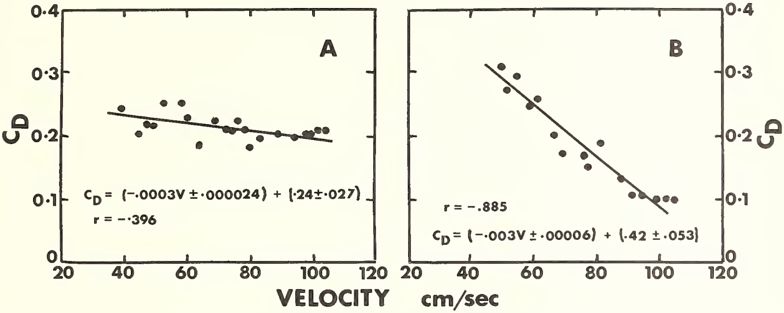
This apparent paradox can be understood in terms of the orientation of these prostheses relative to the flow. All are inclined to the flow: P1–P3 by 45°, and P4 by 20° (Table 2). This means that an increasingly large space develops between the trailing edge of the shell and prostheses as the size of the latter increases (text-fig. 10). As noted in text-fig. 10D, the effect of this gap on flow structure is to increase the turbulence around the rear of the prosthesis, rather like the tandem cylinder effect that I have described for gyrocones (Chamberlain 1976). The drag elicited will obviously depend on the degree of extension. When extension is pronounced, the space will be large and drag high, whereas the converse will hold when little extension occurs. This is precisely what we observe in the drag data for the sequence P1–P3. The beneficial effect of the large prosthesis (P3) is partially negated by the drag produced at the rear of the prosthesis so that the total drag loss is less. For P4 the orientation is only 20°—an inclination too small to produce this effect (note in text-fig. 8A that there is no noticeable diversion of the flow at the rear of the prosthesis). Thus, the full benefit of its large size can be realized, and it is observed to generate the greatest drag loss of all the examples studied.

We can now return to the original question of whether greater extension produces greater drag loss. P1 and P4 should be taken as the appropriate samples on which to base our arguments on this point because only in these two prostheses is the problem described above an insignificant one. P1 is too small to create a large gap, and P4 is too near parallelism with the flow to create a large gap. The drag



TEXT-FIG. 10. Effect of prosthesis orientation on flow structure for model C. Upper row shows profile at trailing edge of shell model. Lower row shows cross-section through shell model and prosthesis. Arrows point to space between trailing edge and prosthesis discussed in text. *A*: P1. *B*: P2. *C*: P3. *D*: flow structure for model C+P3. Turbulence is enhanced by space between trailing edge of shell and prosthesis.

data for these two prostheses in Table 5 give results that seem consistent with our expectations; the larger prosthesis does indeed appear to produce a larger drag reduction. Table 6, however, shows that these results are not statistically significant. This can be taken in two ways: (1) the degree of extension has no measurable effect on drag loss; or (2) there is a relationship, but data in Tables 5 and 6 do not establish it firmly. I prefer the second alternative. I believe that the key here is the unusually high standard deviation for the average drag coefficient of P4 (see Table 5). The reason for this anomalously high standard deviation is shown in text-fig. 11. P4 is the only prosthesis in which drag coefficient can be identified as varying appreciably with velocity. By assuming that drag coefficient is independent of velocity, which is implicit in computing an average drag coefficient, this velocity-related variation is expressed as dispersion around the mean drag coefficient, resulting in a high standard deviation.



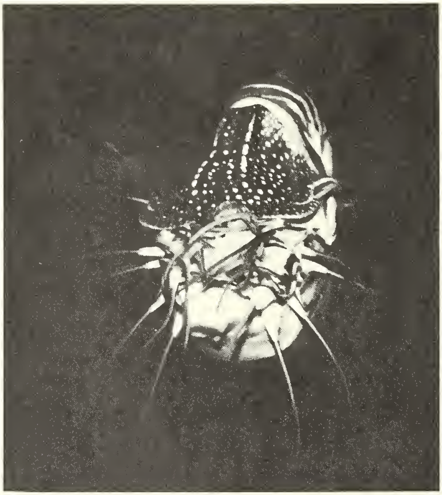
TEXT-FIG. 11. Drag coefficient as a function of velocity for two body prosthesis configurations. *A*: model C + P1. *B*: model C + P4. Each dot represents one constant-velocity tow-tank run. Linear regression lines fitted to data. Regression equations shown on plots. C_D, drag coefficient; V, velocity in cm/sec; r, correlation coefficient.

A better way to treat the data in this case is to analyse the relationship between drag coefficient and velocity. I fitted linear regression lines to the data for both prostheses. The equations for these lines and their correlation coefficients (which are significant at the 95% level according to the procedure given by Till 1974, pp. 86, 87), are shown in text-fig. 11. The slopes and intercepts of the two lines are clearly different, which implies that the hydrodynamic effect of the two prostheses is probably also different, even though the means of the two data sets cannot be statistically distinguished. Thus, from text-fig. 11 it seems that for compressed ectocochliates (and perhaps for others as well) increased body extension may enhance drag reduction, at least at high velocities.

One implication of these considerations is that an ectocochliate may elevate its performance by extending its body as far as possible, especially at high velocity. But in doing so, it must take care to align itself parallel to the flow so that it avoids forming gaps behind the trailing edge of the shell. Proper posture is critical. The specimen shown in text-fig. 3 seems to have achieved this condition, but it would be unwarranted to assume that the data given in text-fig. 11 accurately reflect the benefit this *Nautilus* acquires by this behaviour. The animal's velocity was not measured and this may be of some significance as text-fig. 11 implies, but more importantly, neither shell model nor any of the prostheses incorporate the anatomical details seen in *Nautilus*. How much *Nautilus* profits energetically from such behaviour must remain uncertain until more sophisticated analysis is accomplished.

THE EFFECT OF TENTACLE EXTENSION

Most aquatic animals exhibit several different swimming styles, each of which is used for a specific purpose. Many squids and teleost fish, for example, rely on fin propulsion at slow speeds, but fold their fins against their bodies to reduce drag and conserve energy at high speed (Zuev 1966; Trueman and Packard 1968; Hertel 1966). Ectocochliates may also show a multiplicity of swimming styles. *Nautilus* certainly does. During its peak locomotory periods, the body is extended and the tentacles held in the tapering mass shown in text-fig. 3. When swimming at moderate speeds near the bottom, two tentacles are often extended downward to retain tactile contact with the substrate. At slow speeds, especially when attempting to locate food or to grasp some object, a number of tentacles are extended outward in a search web (see text-fig. 12).



TEXT-FIG. 12. *Nautilus* taking shrimp. Slow movement, tentacles deployed in search web. Wire holding shrimp is seen descending from upper left corner.

It is interesting to reflect on the role of tentacle extension in locomotion and expecially on the additional drag that extended tentacles create. To do this, recourse to experiments like the present ones is fortunately not necessary because an adequate theory exists for the prediction of tentacle drag.

The drag on a single fully extended tentacle can be estimated if we assume that the tentacle is a straight, circular cylinder inclined at some angle of attack (θ) to the flow. Text-fig. 12 suggests that this assumption is not unrealistic. Furthermore, we will say that the tentacle sheath is operating in the separated flow near the shell and hence can be neglected as far as its drag is concerned. Judging from the positions of the sheaths in text-fig. 12, this too is a reasonable assertion. This assumption also has the advantage that we need not concern ourselves with interference drag at the tentacle-body contact. The normal force (F_N) acting on such a tentacle will be given by:

$$F_N = \tfrac{1}{2}\rho V^2 A C_{D_c} \sin^2 \theta \qquad \text{Eq. 1}$$

where ρ is water density; V is swimming velocity; A is frontal area; and C_{D_c} is the drag coefficient of a circular cylinder held perpendicular to the flow (see Taylor 1952; Hoerner 1965). Substituting $A = dh$ (diameter·height) and drag force (D_F) $= F_N \sin \theta$, we can write:

$$D_F = \tfrac{1}{2}\rho V^2 dh C_{D_c} \sin \theta \qquad \text{Eq. 2}$$

Since C_{D_c} for a perpendicular cylinder $\approx 1{\cdot}0$ in the present Reynolds number range; $\rho = 1{\cdot}027$ gm/cm³; and since tentacle length ≈ 9 cm, tentacle diameter $\approx 0{\cdot}3$ cm, and $\theta \approx 135°$, in the adult animals observed at the New York Aquarium, equation 2 becomes:

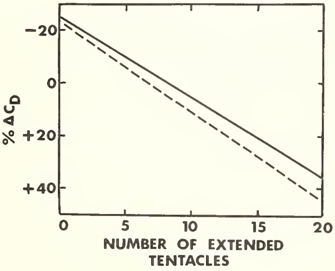
$$D_F = 0{\cdot}98 \text{ gm/cm } V^2. \qquad \text{Eq. 3}$$

We can now calculate the drag force produced by this tentacle (or any number of similar tentacles by simply multiplying the right side of equation 3 by this number), and compare the result with the drag generated by the shell and extended body. Text-fig. 13 shows the outcome of these computations expressed in terms of drag coefficients. The parameter plotted on the ordinate ($\%\Delta C_D$) should be understood as the change in drag coefficient produced by a fully extended body with a specific number of extended tentacles (read on the abscissa) relative to the drag coefficient of the empty shell, i.e.

$$\%\,\Delta C_D = 100 \cdot [(C_{D_{s+b+t}}/C_{D_s}) - 1]$$

where C_{D_s} is shell drag coefficient; and $C_{D_{s+b+t}}$ is the drag coefficient of the shell+body+tentacle combination. A negative value for this parameter means that $C_{D_{s+b+t}}$ is less than C_{D_s}, while a positive value means that it is greater than C_{D_s} (remember that hydrodynamic efficiency increases as $\%\,\Delta C_D$ takes on increasingly negative values). The calculation of per cent drag coefficient change is based on a C_{D_s} for *Nautilus* of 0·5 (Chamberlain 1976), and incorporates the assumption that correct body extension (without protrusive tentacles as in text-fig. 3) provides a reduction of about 25% in total drag (−0·25 on ordinate in text-fig. 13). While the present tow-tank data cannot be used to pin-point the effect of body extension for *Nautilus*, as noted above, it seems unlikely in view of the similarity in the degree of body extension between model $C+P4$ and the *Nautilus* in text-fig. 3, that *Nautilus* can achieve a drag reduction in excess of 25%. It may well be less, but I think that 25% represents a reasonable upper limit, and so I have chosen this value as a basis for constructing the plot in text-fig. 13. If the true reduction is less than 25%, the *Nautilus* curve will simply be shifted downward by the difference between the actual value and my 25% estimate.

The main point made in text-fig. 13 is that tentacle drag is an important component of total drag. Extending only two tentacles while swimming, as *Nautilus* often does, results in a drag increase of



TEXT-FIG. 13. Per centage change in drag coefficient ($\%\,\Delta C_D$) caused by extension of tentacles outward from body relative to drag coefficient of empty shell. When number of extended tentacles = 0, $\%\,\Delta\, C_D$ = change in C_D of shell alone due only to body extension. See text for further discussion. Solid line—adult *Nautilus* as described in text. Dashed line—model C+P4 with degree of tentacle extension as for *Nautilus*.

about 7%, while extending ten tentacles as in text-fig. 12 results in about 5% more drag than if body and tentacles were completely retracted into the shell. When twenty tentacles are extended drag is about 37% greater than if the animal were completely retracted, and 62% greater than if its body were properly extended. Surely, it cannot be a surprise that as a *Nautilus* increases its speed it retracts its tentacles. This aspect of *Nautilus* behaviour thus seems to derive from the same respect for conservation of propulsive energy that impels fish and squids to fold their fins at high speed. There is, however, one important difference between *Nautilus*, fish, and squids in this regard. Because of its relatively poor eyesight (see Packard 1972), *Nautilus* apparently relies in many situations on the sensitivity of its tentacles to provide information about its surroundings. When the tentacles must be retracted to maximize speed, *Nautilus* would seem to lose a significant portion of the sensory input needed to judge position, direction, and speed, perhaps to the point where an animal is effectively swimming blindly at peak speeds. Qualitative observations made on five specimens at the New York City Aquarium suggest that at its highest speeds, *Nautilus* 'crashes' more frequently into obstacles than when swimming slowly. With their anterior, camera-type eyes, fish do not have this problem (although in a few species, like angelfish, some fins may have a tactile function). Squids seem to be intermediate. Like fish they have camera eyes, but like *Nautilus* the eyes are far back on the body. Undoubtedly, the same considerations apply to fossil ectocochliates. They too may have had difficulty in control at high speed.

The dashed line in text-fig. 13 is for model $C+P4$ with hypothetical extended, cylindrical tentacles, for which the tentacles bear the same relative size (with respect to shell) as for *Nautilus*. It shows that in animals with compressed shells, the effect of tentacle extension is even more severe than for *Nautilus*. This is because the drag coefficients of these shells are small so that tentacle drag makes up a larger fraction of total drag.

SUMMARY

Studies of the hydrodynamic properties of body extension in ectocochliates by tow-tank and flow-visualization experiments on scale models of shells and cephalopod bodies allow a number of conclusions to be drawn:

1. Extension of the body from the aperture produces a small ($\sim 10\%$), but measurable decrease in drag. In compressed shells, and perhaps in a few others, e.g. *Nautilus*, the change may have been as high as $\sim 25\%$. Thus, body extension may have had an important beneficial effect in the locomotion of some ectocochliates, but for most was probably of relatively minor significance.
2. The extent of drag reduction produced by body extension depends on posture. To be most effective, the body must be extended parallel to the flow direction (direction in which animal swims), extended as fully as possible, and extended so that no gaps are allowed to form between the body and trailing edge of the shell. *Nautilus* (see text-fig. 3) is capable of this kind of extension.
3. Extending tentacles outward into the flow as *Nautilus* often does (see text-fig. 12) can greatly increase drag, and completely overcome the beneficial effect of the extended body. In *Nautilus* this problem is minimized by retracting the tentacles into their protective sheaths during periods of peak locomotory activity. This behaviour is analogous to fin folding seen in many fish and squids at high speed. But unlike fish and squids, *Nautilus* evidently loses a significant portion of its spatial sensory input in this process, so that at its high speed, *Nautilus* is much less adept than fish or squids are at theirs.

It would appear that, as with many scientific controversies, the hydrodynamic effect of body extension actually represents a compromise between opposing views; in this case, of such researchers as Schmidt and Geczy who envisioned body extension to be of major importance in drag production, and myself when I advocated the antithesis in my 1976 paper.

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Institute) for their guidance and friendly co-operation during the course of the experiments. I thank Dr. G. D. Ruggieri, S.J., director of the New York City Aquarium, for permitting me to study the *Nautilus* specimens in his care. The assistance of A. A. S. Chamberlain, R. B. Chamberlain, and A. Shapiro (Brooklyn College) was instrumental in completing the experimental portion of the work. This research was supported by a grant from the Research Foundation of the City University of New York.

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SHALLOW-WATER CRETACEOUS BRACHIOPODS FROM ROCKALL BANK, NORTH ATLANTIC

by GEORGE E. FARROW *and* ELLIS F. OWEN

ABSTRACT. A shallow-water fauna of terebratulide brachiopods, bryozoans, and bivalves is described from the western margin of Rockall Bank, occurring in phosphatized ferruginous sandstones of 'greensand' facies. '*Carneithyris*' *rockallensis* sp. nov. suggests a date of Upper Cretaceous age, possibly as young as Maastrichtian. A glacial origin is possible.

THREE rock dredge hauls from the western margin of Rockall Bank, text-fig. 1, have yielded the first recorded Mesozoic shelf fauna from the North Atlantic. They were taken during Cruise 4/78 of R.R.S. *Shackleton* whilst the vessel was engaged in an underwater television and dredging study of carbonate sedimentation on the northern part of the Bank. Fossiliferous material was obtained from the following stations:

Station	Lat.	Long.	Water depth	Material collected	Repository
69/2	57° 00·3′ N.	15° 10·8′ W.	474 m	Subrounded phosphatic cobbles; loose fossils	BM
71/2	57° 09·2′ N.	14° 57·6′ W.	387 m	Individual phosphatized terebratulides; broken ferruginous sandstone	HM × 1030 (TS 69/001–12)
72	57° 19·5′ N.	14° 51·6′ W.	360 m	Tabular slabs of terebratulides in sandstone	BM; HM × 10743, 10744, 10746

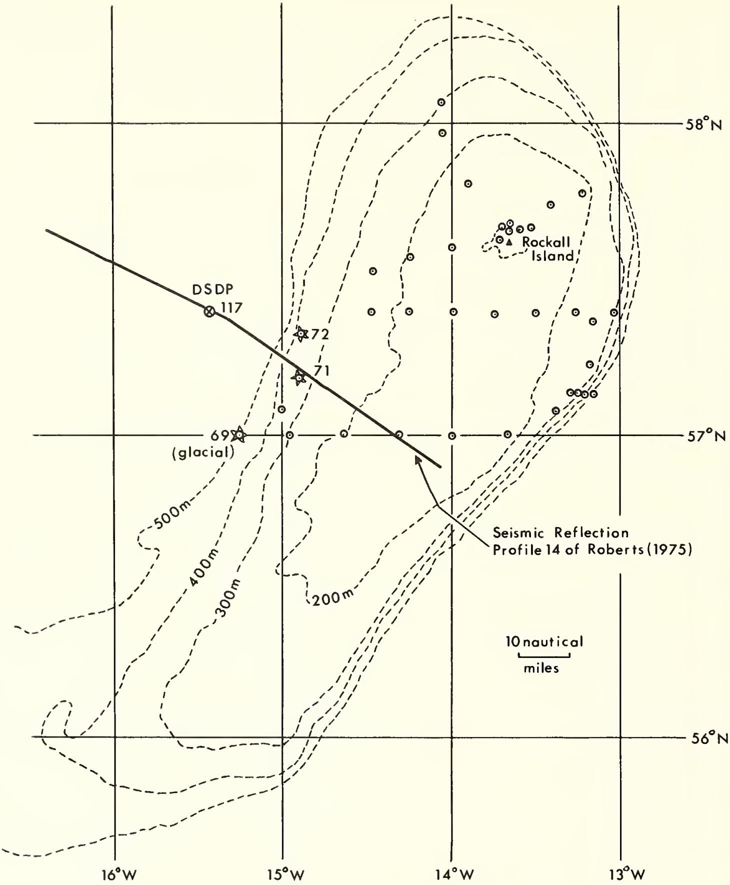
BM = British Museum (Natural History), Palaeontological Collections; HM = Hunterian Museum (University of Glasgow), Geological Collections

At station no. 69 the dredge brought up a spectacular variety of obviously glacial material (quartzite, arkose, phyllite, pumice, granite) in addition to the more frequent fossiliferous phosphate, which was subrounded. Further north-east, however, at stations nos. 71 and 72, nothing was recorded except blocks of phosphatic sandstone and large, extremely well-preserved, highly polished, individual fossil terebratulides (text-fig. 3). Smaller terebratulides may also have been present, but these would have been lost during hoisting because of the relatively large mesh of the dredge bag.

It is always difficult to be certain whether boulders dredged from high-latitude shelves and banks represent the solid geology or have been plucked from a surface strewn with ice-rafted drop-stones. This problem is acute on the margins of Rockall Bank, for Belderson *et al.* (1973, p. 217, fig. 4) and Roberts (1975, p. 456, fig. 5) show that iceberg plough marks are often encountered between 500 and 150 m. However, the following observations are not inconsistent with the interpretation of a solid substrate for stations nos. 71 and 72: all the material was of a single rock type; none shows evidence of striation or rounding and some blocks show fresh fractures; no 'tide-marks' free of epifauna were present around the base of blocks, such as would indicate partial burial in sediments.

On Rockall Bank, material associated with iceberg plough-marks is generally basaltic (Belderson *et al.*, 1973, p. 220); on the Scottish shelf, boulders are often striated and cobbles rounded or subrounded, including a wide range of types (just as at station no. 69). It cannot be ruled out, therefore, that solid Cretaceous phosphatic sandstones crop out on the western flank of Rockall Bank in the region of 59° 9–19′ N. and 14° 52–58′ W., and that grounding icebergs moving southwards have dispersed the material more widely.

[Palaeontology, Vol. 23, Part 2, 1980, pp. 463–470.]



TEXT-FIG. 1. Map showing the location of the three dredge stations yielding fossiliferous Upper Cretaceous sedimentary rocks. [Bathymetry from I.O.S. chart of north-east Atlantic: line of seismic reflection profile from Roberts (1975, fig. 12, p. 472); other stations plotted during R.R.S. *Shackleton* cruise 4/78 did not yield any Cretaceous material.]

TEXT-FIG. 2. Mass of large bryozoan specimens in pseudoconglomeratic phosphate block, dredged from station no. 69/2, × 1·25.

Identification and age of the fauna

Brachiopods constitute the most spectacular element in the fauna, though they are equalled, if not outnumbered, by large quantities of a stout, ramose bryozoan (text-fig. 2) unlike anything with which we are familiar in the British Cretaceous. Two poorly preserved internal moulds were identified as follows:

1. Fragment of a bivalve internal mould reminiscent of the Crassatellacea but with a posterior adductor scar unusually close to the umbo.
2. Internal mould of an arcticacean bivalve with no hinge or muscle scars preserved, similar in shape to some Cretaceous species.

Phosphatic blocks are noticeably nodular, even conglomeratic, in appearance. This is, in part, caused by projecting fossil Bryozoa and, in part, the result of present-day biological erosion. They are strikingly similar to the Cenomanian glauconitic calcarenite illustrated by Laughton, Berggren *et al.* (1972, from DSDP 111, pl. 1B, p. 85 and pl. 9, p. 101) which is a phosphatized hardground.

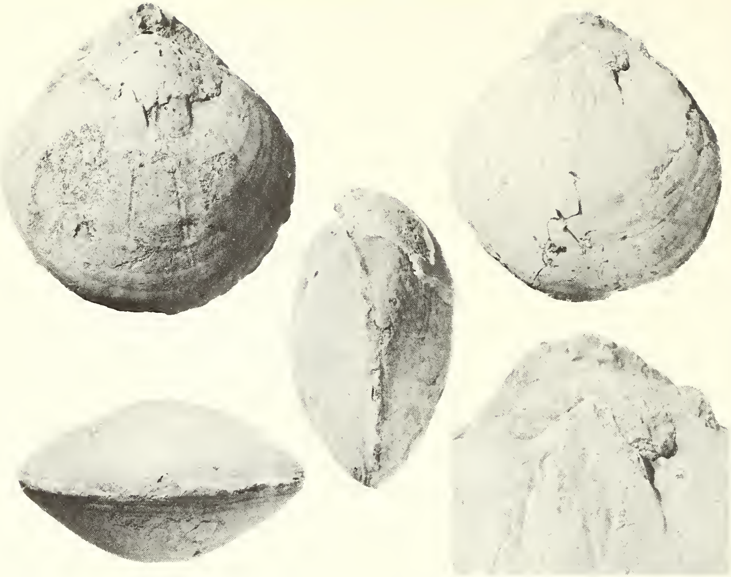
A block of highly glauconitic, phosphatic sandstone, 16 × 20 cm, contained a fauna of large, subcircular, acutely biconvex terebratulides which at first were thought to be assignable to the genus *Cyrtothyris*, originally described by Middlemiss (1959) from the Upper Aptian of Upware, Cambridge. A more critical examination involving transverse serial sections of one of the specimens suggested a close affinity to the genus *Carneithyris*, which Sahni (1925*a*) described from the Upper Chalk, *Belemnitella mucronata* Zone, Norwich, Norfolk. There are, however, minor features within the internal structure of the Rockall specimen which are regarded as atypical of Sahni's *Carneithyris*, and it is for this reason that a broader interpretation of the genus is used for the species described here as '*Carneithyris*' *rockallensis* sp. nov.

SYSTEMATIC DESCRIPTIONS

Superfamily TEREBRATULACEA Gray, 1840
Family TEREBRATULIDAE Gray, 1840
Subfamily CARNEITHYRIDINAE Muir-Wood, 1965
'*Carneithyris*' *rockallensis* sp. nov.

Text-figs. 3, 4

Description. Large pentangulate to subcircular carneithyride, 59·1 mm long, 56·4 mm wide, and 31·6 mm thick. Evenly biconvex, rectimarginate. Pedicle valve with short massive, slightly incurved umbo, truncated by a large subcircular foramen with fairly distinct permesothyridid beak-ridges. Deeply incised, elongate adductor muscle



TEXT-FIG. 3. '*Carneithyris*' *rockallensis* sp. nov. Lower Maastrichtian (dredged) at station no. 71/2, on north-western slope of Rockall Bank. Left and centre, holotype (B.M. specimen no. BB 76583) in dorsal, lateral, and anterior views, × 1. Right, B.M. specimen no. BB 76584: above, showing general pentangulate outline and position of subparallel muscle scars just anterior to dorsal umbo, × 1; below, umbonal region to show faint median ridge between the muscle scars, × 2.

scars lie centrally placed, one on either side of a low median depression on the floor of the brachial valve. The faint impressions of numerous branching pallial markings are visible on the surface of internal moulds.

A massive cardinal process, semicircular in transverse outline, extends well into the pedicle valve, becoming more elongate and peg-like.

Low, thickened, ventrally concave hinge-plates, with well-developed inner and outer socket-ridges, diminish rapidly and incline dorsally. Rounded hinge-teeth with poorly developed accessory denticulae become subquadrate to broadly triangular in transverse outline.

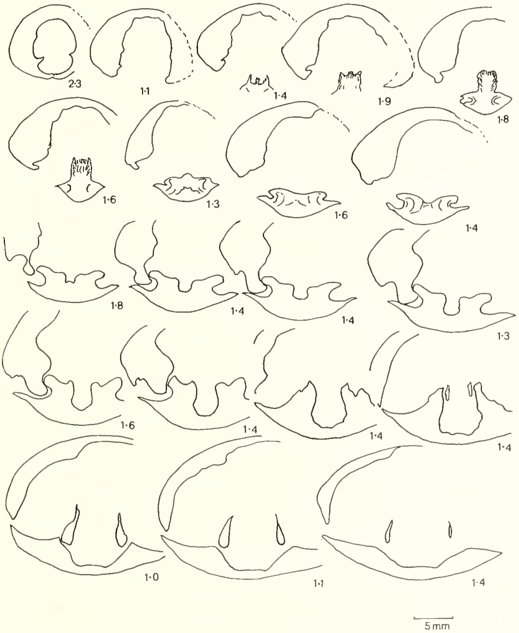
Thickened, but elongate, subparallel crural processes are given off from the distal ends of the hinge-plates.

Remarks. '*Carneithyris*' *rockallensis* sp. nov. differs from the type species, *Carneithyris carnea* (J. Sowerby) in having a more pentangulate general outline, larger pedicle foramen, more distinct beak-ridges, and slightly more produced and incurved umbo.

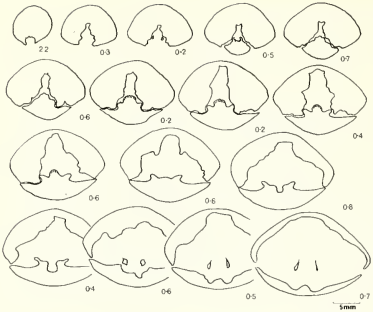
In transverse outline it is seen to have a similar degree of thickening of the shell to that of *C. carnea*, particularly in the umbonal region, and the same general transverse outline of teeth and sockets. It also has similarly developed hinge-plates with well-developed inner and outer socket-ridges, but in '*Carneithyris*' *rockallensis* these remain low and slightly concave on their ventral surface. They extend well into the body cavity where they begin to incline steeply towards the dorsal valve, a character also observed in transverse serial sections of *Oleonithyris harlani* (Morton) from the Paleocene of New

Jersey, U.S.A. (Feldman 1977, p. 93). This stage is reached earlier in the development of the shell in *C. carnea*. Nevertheless, the general pattern and development of the internal characters of the two species, as seen in serial sections (text-figs. 4, 5), shows very clearly that the two forms have a great deal in common.

The predominance of the massive cardinal process with its characteristic bulbous shape, distinguishes the Carneithyridinae from other Upper Chalk Terebratulidae and Sahni (1925*b*) used these and certain hinge characters to distinguish morphological variants which he split into genera and species. Recently, Asgaard (1975) in an exhaustive study of Upper Chalk Carneithyridinae, has shown that Sahni's interpretation of these characters was too narrow, suggesting that he had not understood the true range of variation within the Carneithyridinae as a whole. His results, though somewhat advanced for the time, cannot now be applied stratigraphically with any degree of confidence. It can be seen, however, that certain morphological differences do exist between forms which Sahni had described as *Magnithyris*, *Carneithyris*, and *Chatwinothyris*. One of these differences lies in the absence, in *Magnithyris magna* Sahni, of a marked median ridge or low septum separating the muscle scars on the floor of the brachial valve and this character is also absent in transverse serial sections of '*C.*' *rockallensis* sp. nov. shown here (text-fig. 4). The general outline of *Magnithyris*



TEXT-FIG. 4. Twenty transverse serial sections through the umbo of a specimen of '*Carneithyris*' *rockallensis* sp. nov. obtained from a block of sandstone dredged from the north-western slope of Rockall Bank.



TEXT-FIG. 5. A series of sixteen transverse serial sections through the umbo of a specimen of *Carneithyris carnea* (J. Sowerby) from the Upper Senonian, *Belemnitella mucronata* Zone, Portrush, Northern Ireland.

magna, the species which Sahni had selected as type species of the genus, and that of '*C.*' *rockallensis*, on the other hand, are very similar and the pedicle foramen in both forms is large, circular, and with fairly well-marked permesothyridid beak-ridges.

Similarly, minor differences of internal structure between *C. carnea* and *Chatwinothyris* are also discernible from a comparison of transverse serial sections. Steinich (1965), in a description of brachiopods of Maastrichtian age from Rügen in northern Germany, selected a specimen which he identified as *C. subcardinalis* Sahni, the type species, giving a series of fifteen serial sections (fig. 28, p. 42) which have been copied and figured here (text-fig. 6) for comparison. The mode of development of the cardinal process, more acutely ventrally inclined hinge-plates and less well-developed median ridge on the floor of the dorsal valve, suggest a closer affinity between this species and '*C.*' *rockallensis* sp. nov.

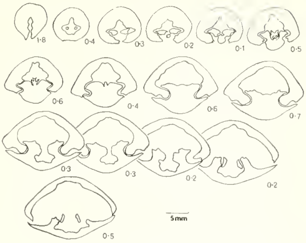
Unfortunately no direct comparison of transverse serial sections can be made between '*C.*' *rockallensis* and *M. magna* due to the lack of suitable material of either species and it may subsequently be found that the two forms are more closely affined than was at first envisaged.

While admitting that there is insufficient evidence for an *in situ* origin for the sandstone block examined, it is felt that the brachiopods described here are of undoubted Upper Cretaceous age and, as a result of comparison of internal structures with those of species considered to be of Maastrichtian age, the species described here as '*C.*' *rockallensis* sp. nov. is tentatively assigned to the Lower Maastrichtian.

Significance of the brachiopod fauna

The presence of a carneithyrid terebratulide fauna within the assemblage dredged from the Rockall Bank indicates an Upper Cretaceous age or younger. Clearly the material might well have been transported but the brachiopod specimens extracted from the block of sandstone described here were well-preserved internal moulds and a few single specimens with the remains of thick calcareous shells. None of the specimens was worn nor did they appear to have been rolled.

The genus *Carneithyris* is well represented in the British Upper Chalk, *mucronata* Zone, from the Norwich district of Norfolk from whence it was first described by Sahni (1925*a*). Species referable to this genus have also been collected from the highly glauconitic beds of equivalent age at Portmuck, Co. Antrim, and also from the Top Flinty beds of the Belfast area, Northern Ireland. Hancock (1961, p. 26) and Wood (1970, p. 78) consider the upper mass of White Limestone from the same district to be of Senonian age, but suggest that Maastrichtian beds were probably deposited within the Belfast area and have subsequently been eroded prior to the extrusion of the Tertiary Basalts.



TEXT-FIG. 6. A copy of fifteen serial sections through a specimen of *Chatwinothyris subcardinalis* Sahni from the Lower Maastrichtian of Rügen, North Germany (after Steinich, 1965, fig. 28, p. 42).

CONCLUSIONS

Shallow-water sediments with claimed ages from Upper Cretaceous to Eocene have been dredged from both sides of Rockall Bank and from the western slopes of Porcupine and Hatton Banks (Bailey and Haynes 1974; Watts *et al.* 1975; Dobson *et al.* 1976). Doubt may still exist over the *in situ* nature of particular individual occurrences, for a glacial origin is possible, but the regional totality of records is becoming impressive. The sediments include oolitic limestone from 59 N. (Watts *et al.* 1975, p. 642)—a surprisingly high latitude considering the probable Maastrichtian palaeolatitude of 40 N. (Smith *et al.* 1973, fig. 7), a fact that would be made more difficult to explain by invoking a glacial origin; arkose and lithic conglomerates (with a probable southerly derivation), and condensed phosphatic greensands of a high-energy environment containing a brachiopod fauna and also a hardground aspect (this paper).

Previous estimates of age have been based on either pelagic foraminifera from slope sediments (Dobson *et al.* 1976) or on dubious dinoflagellates (Watts *et al.* 1975). This record of '*C.*' *rockallensis* gives the first reliable age, Maastrichtian, for the shallow-water facies—an age slightly younger than that obtained for the Helen's Reef microgabbro intrusion, dated at 81 ± 3 m.y. (Harrison *et al.* 1975, p. 71). Shallowing of the Bank may have been associated with the intrusive event, or more plausibly could have resulted from general Maastrichtian eustatic regression (Hancock 1975, p. 104), the resulting facies representing the nearshore equivalents of the offshore chalks commonly recorded off the mainland massifs (e.g. Lapierre 1975; Hancock 1975, fig. 3).

Both the fauna and the lithology of the Rockall material show a close affinity with the Northern Ireland sequence, but are different from the East Greenland succession which is dominated by coarse clastics (Donovan 1957).

As a result of the rapid westward drift and the concomitant subsidence of Orphan Knoll (300 miles south of Rockall Bank) in the Senonian–Palaeocene interval, the Maastrichtian in that area is of pelagic facies (Laughton and Berggren 1972, p. 52), whereas the Rockall Plateau evidently remained as a stable block and may have had a very similar Cretaceous history to that of Northern Ireland.

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AN *IN SITU* HERMIT CRAB FROM THE EARLY MIOCENE OF SOUTHERN NEW ZEALAND

by FIONA M. HYDEN *and* JACQUES FOREST

ABSTRACT. An Early Miocene (Burdigalian) hermit crab preserved within a struthiolariid gastropod shell is described. The specimen, here designated *Pagurus clifdenensis* sp. nov., has close affinities with the Recent species *P. spinulimanus* (Miers) which is common in New Zealand waters.

FOSSIL hermit crabs (pagurids) are rarely preserved *in situ* since they vacate their shelters (usually a gastropod shell) prior to death (Schäfer 1972, p. 131). Poor calcification and delicate skeletal structure of the cephalothorax renders them highly susceptible to taphonomic loss, and in almost all cases fossil specimens are represented only by the heavily calcified and robust chelipeds (Glaessner 1969). However, one *in situ* well-preserved pagurid has been found in a gastropod shell (*Struthiolaria subspinosa* Marwick, fig. 1), within a sequence of richly fossiliferous silty fine sandstones at Clifden, Southland, New Zealand. The rich associated molluscan fauna suggests a middle-inner neritic depositional environment.

SYSTEMATIC PALAEONTOLOGY

Family PAGURIDAE Latreille, 1802
Subfamily PAGURINAE Latreille, 1802
Genus PAGURUS Fabricius, 1775
Pagurus clifdenensis sp. nov.

Text-fig. 1–3

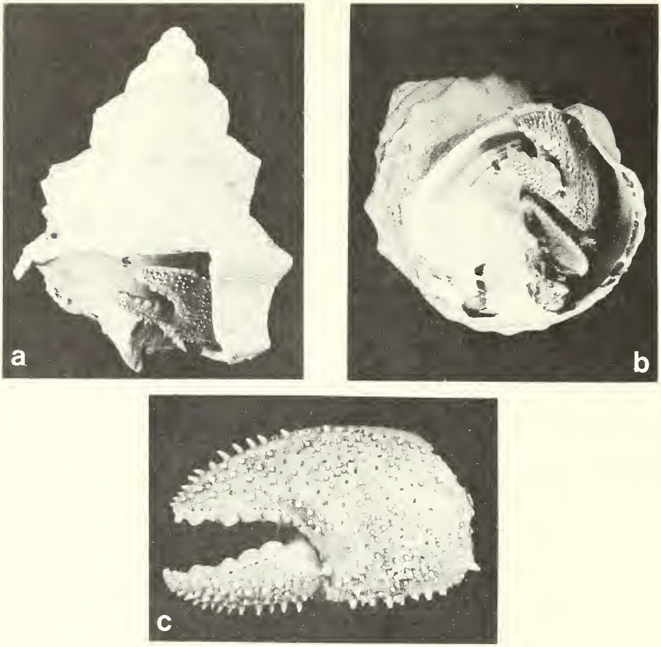
Holotype. Specimen No. O.U. 11797 in the Department of Geology, University of Otago, New Zealand. Parts of left and right chelipeds and second and third periopods exposed *in situ* in gastropod (*S. subspinosa* Marwick).

Stratigraphic Occurrence. Calamity Point Sandstone, Nga Pari Formation, south bank of Waiau River, Clifden, New Zealand (Wood 1969); Altonian local stage (Early Miocene).

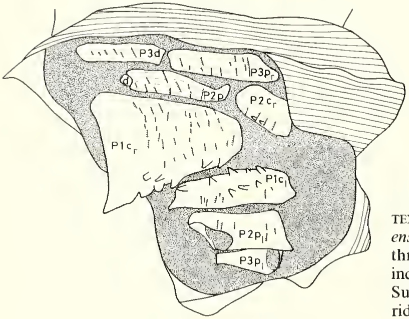
Diagnosis. Right cheliped larger than left; both covered with large, cone-shaped tubercles on dorsal surface; smaller and more numerous than in *P. spinulimanus*. Double row of molariform teeth on opposable faces of right chela; thoracic appendages covered with piliferous holes and striations. Manus of left cheliped longer than in *P. spinulimanus*.

Description. Right cheliped: Carpus has convex dorsal surface, bearing short, transverse, piliferous striae; row of large teeth on mesial border (text-fig. 2). Manus suboval, length 13·2 mm, width 7·7 mm, dorsal surface slightly convex. External and mesial margins of propodus lined with cone-shaped teeth, some of them broken; dorsal surface ornamented with numerous, evenly distributed, acute tubercles and innumerable minute perforations (5 μm and 12 μm in diameter). Double row of large, molariform teeth along opposable faces of fingers, bordered by a series of composite, indented perforations (text-figs. 1, 3*a*). Left cheliped (text-figs. 1, 3*a*): Propodus elongated, length 9·7 mm, width 3·6 mm; manus shorter than dactylus. Dorsal surface ornamented with cone-shaped tubercles and piliferous holes as in right cheliped; external margin also lined with broken cone-shaped teeth.

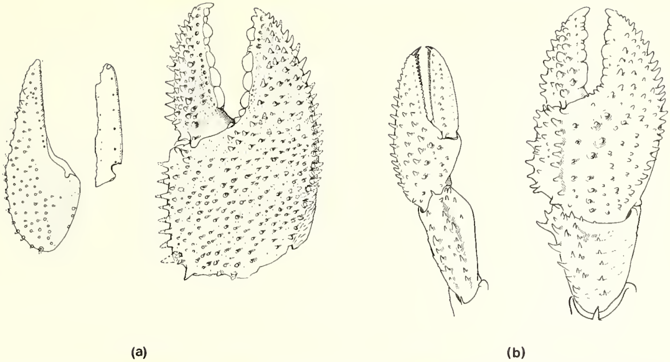
[Palaeontology, Vol. 23, Part 2, 1980, pp. 471–474.]



TEXT-FIG. 1. *Pagurus clifdenensis* sp. nov. within damaged gastropod shell (*Struthiolaria subspinosa* Marwick). (*a*) View of part of right cheliped; × 2. (*b*) Oblique view showing right and left cheliped in damaged aperture; × 2. (*c*) Propodus and dactylus of right cheliped; × 4·5.



TEXT-FIG. 2. Camera lucida drawing of *Pagurus clifdenensis* sp. nov. with part of gastropod shell removed. First three periopods (P1–P3) exposed in matrix (stippled), including carpus ‘c’, propodus ‘p’, and dactylus ‘d’. Suffices refer to right ‘r’ and left ‘l’ periopods. Transverse ridges possess piliferous holes, × 4.



TEXT-FIG. 3. Camera lucida drawing of fossil and Recent pagurids: (*a*) Right and left chelipeds (propodus and dactylus) of *Pagurus clifdenensis* sp. nov. (Miocene), ×4. (*b*) Right and left chelipeds of Recent New Zealand species, *Pagurus spinulimanus* (Miers), ×2·5. All illustrations in dorsal view, except dactylus of left cheliped of *Pagurus clifdenensis*, in ventral aspect.

Small indentations along entire length of straight cutting edge of fixed finger; line of six piliferous alveoli, bordering opposable face of dactylus (text-fig. 3*a*). Second and third periopods lack teeth or spines but they possess several transverse piliferous striations (text-fig. 2); propodus rounded in cross-section.

Discussion. Though most of the significant taxonomic features cannot be observed in the fossil specimen, details of the thoracic appendages are very similar to those of the Recent pagurid, *P. spinulimanus* (Miers) (text-fig. 3*b*). *P. spinulimanus* has previously been described as *Eupagurus edwardsi* Filhol, *E. intermedius* Lenz (cf. Thompson 1930, p. 271) or *E. norae* Chilton. The Recent New Zealand pagurid fauna is currently being revised by J. Forest and M. de Saint Laurent, and both *P. clifdenensis* sp. nov. and *P. spinulimanus*, together with the larger, related Recent species *P. rubricatus* Henderson, will be moved to a new genus.

Size and distribution of perforations on the periopods of *P. clifdenensis* suggest that they were covered with very thick, rather short hairs, rather like *P. spinulimanus*, concealing the teguments except at the apex of tubercles and teeth. Holes and transverse striations on the fossil correspond to the much longer hairs observed in similar areas of *P. spinulimanus*. Moreover, a row of alveoli on the cutting edge of the dactylus (left cheliped) in *P. clifdenensis* most probably represent the insertion of small comb-like teeth which occur in *P. spinulimanus*.

P. spinulimanus is common in the New Zealand region, particularly around the Auckland Islands, to the north of the North Island, near the Chatham Islands, to the east of the South Island, and on the Otago shelf. It is most common on muddy sand substrates at depths of between 20 and 120 m.

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